XII. *Studies in the Morphology of Spore-producing Members.—Equisetineæ and Lycopodineæ.*

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[Plates 42–52.]

INTRODUCTION.

The observations of Hofmeister stand, in their broad outlines, as the foundation of the morphology of archegoniate plants. It will be assumed that readers will accept in the main the homologies which, on the basis of those observations, he recognized between the corresponding parts of the Bryophyta, Vascular Cryptogams, and Gymnosperms; it will also be assumed that, whatever may have been the circumstances which led to it, antithetic alternation was brought about by elaboration of the zygote so as to form a new generation (the sporophyte) interpolated between successive gametophytes, and that the neutral generation is not in any sense the result of modification or metamorphosis of the sexual, but a new product having a distinct phylogenetic history of its own. Those who accept this view will keep distinct in their minds the sexual generation or gametophyte on the one hand, and the neutral generation or sporophyte on the other, whatever their variations, either in relative size or in physiological dependence; and they will recognize that no homologies are to be admitted between them or their parts. Clear conceptions on these points are absolutely essential, if there is to be real progress in comparative morphology; though the study of either generation may shed side-lights upon the problems relating to the other, the two alternating generations must be treated apart, so long as the main conclusions of Hofmeister continue to be accepted.

The assumption above made as to the origin of antithetic alternation is based upon a general comparison of living plants, which leads to the conclusion that, of the two alternating generations, the sexual generation (the oophyte or gametophyte) was the original one: that subsequently a neutral (the sporophyte) was produced as a stage gradually interpolated between the successive sexual generations; and that this new growth was produced, not by mere modification of the oophyte, or of a part of it, *but by amplification of the product of sexuality—the zygote;* by its sub-division into numerous

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cells the effect of a single sexual process is distributed over the parts produced, these parts, when isolated, may be styled the *spores*, or, to distinguish them from other unicellular organs of propagation, they are designated by the special term "*carpospores*." Further comparison of living forms leads to the conclusion that there followed upon the increasing size of the sporophyte a *progressive sterilization* of its tissues, so that only a part of those tissues continued to be sporogenous; this may be most readily illustrated by reference to the Bryophyta (see below, p. 485, &c.), a series of plants in which progressive sterilization of the tissues of the sporophyte appears to have been closely connected with its increasing size and structural complexity. The series is, however, characterized by the simple external form of the sporophyte, and by the further fact that the sporogenous tissue of each individual sporophyte is normally a continuous mass; accordingly, the recognition of the progressive sterilization is in them comparatively easy.

Progressive sterilization seems also to have played an important part in the evolution of the Vascular Cryptogams; in these, as we see them at the present day, the proportion of sporogenous tissue to vegetative tissue is comparatively small; the sporogenous cells are commonly separated into small masses, or are distributed singly; in fact, the sterilization appears to have progressed much further in the Vascular Cryptogams than in the Bryophyta; the external form, also, is much more complex, owing to the presence of appendicular organs. But though it may be more difficult to trace the steps of sterilization in the living Vascular Cryptogams, owing to the process having been more completely carried out, the experience gained from study of the Algæ and Bryophyta should direct the line of observation into this channel, and occasion to note its effects will frequently arise in subsequent pages.

The adoption of the foliar habit as seen in the sporophyte of Vascular Cryptogams, together with the elaboration of a subterranean system for absorption, brought with it very great advantages; the physiological independence of the sporophyte was thereby secured, and it accordingly assumed a more permanent character and longer life. Considering the greatness of the advantage thus gained, and the remote period of the past at which the step must have been taken in any one of the several series of vascular plants, it is intelligible enough that connecting links, showing how the appendicular organs were first acquired, and how the transition from a continuous archesporium to one consisting of isolated cells or cell-groups took place, should be few and uncertain among the plants of the present day. It has been remarked that the gap between the Bryophyta and the Vascular Cryptogams is the widest in the whole vegetable kingdom. On the one hand are plants with a dependent sporophyte of simple external form, with a continuous sporogenous mass, and having the sporogenous tissue in large proportion as compared with the sterile tissue; on the other, plants with the sporophyte physiologically independent, with complex external form, and sporogenous tissues in isolated masses, or appearing as isolated cells, and with the sterile tissue exceeding it greatly. To bridge over the gap between plants with characters thus widely divergent is the most clearly outstanding problem of morphology. Hitherto, fossils have helped but little in this direction: it therefore appears that investigators must depend mainly upon comparison of living forms. It is not to be expected that even the most diligent study and comparison of these can do more than give suggestions as to the solution of the problem; but if the view above propounded be steadily maintained, and the more complex sporophyte be regarded as a derivative by partial sterilization, and vegetative amplification of simpler original forms, the gulf would appear a less serious one than it is at present commonly believed to be.

The most important additions to knowledge of the Vascular Cryptogams in recent years have related to the oophyte and sexual organs, and to the development of the embryo. While the importance of these is duly appreciated, I may remark that I have not complete confidence in phylogenetic conclusions based upon the vegetative characters of the gametophyte; that generation is certainly very plastic in its form, as witness the various types of prothallus in the genus *Lycopodium*, where the mature sporophyte remains much more constant in character. The question of the relative value of the characters of the two generations for purposes of comparison, in those plants which show conspicuous alternation will be discussed more fully towards the close of this memoir; in the meanwhile it may be stated that while due prominence will be accorded to the sexual generation, the characters of the neutral generation will here chiefly engage our attention, for it is believed that a widely extended study of the morphology of spore-production is specially needed at the present juncture; not only should a re-examination be made of sporangia already investigated by others, but also observations on such rare forms as have not hitherto been fully studied from the point of view of development.

The chief reasons for attaching special weight to the comparative and developmental study of spore-producing organs are as follows. Spore-production was undoubtedly the first office of the sporophyte, and to it practically the whole of the sporogonium was originally devoted; the sporogonium of the simpler Liverworts illustrates what was probably the primitive condition before the vegetative system of the sporophyte appeared. Spore-production is still, even in the most complex of the higher forms, the end to which the whole vegetative system tends. In the life-cycle of the vascular plants and Bryophyta of the present day the production of spores is a regularly recurring event,* and there is every reason to believe that it was regularly repeated throughout the course of their evolution. The spore-producing members, whatever their form, may therefore be styled *primary* as regards the history of descent, and the sporogenous cells which they contain are to be viewed as, at least, the functional, and presumably also the morphological representatives, which survive from the original connected sporogenous mass.*

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* Exception must be made in the case of those few plants which show the phenomenon of apospory, or in which propagation is conducted in a vegetative manner only; both of these conditions have probably been acquired at a comparatively late period.

But the case is different with the vegetative organs of the sporophyte, such as axis, leaf, and root; on comparative grounds it may be concluded that these owed their origin to that progressive sterilization and amplification above alluded to; that a vegetative period, often of considerable length, has thus been intercalated between the fertilization of the ovum and the production of the spores, and thereby the date of production of the spores deferred. However great may be the size of the vegetative organs, the complexity of their form and internal structure, and however long the time of their duration, they should still be placed in a subordinate position, and may be styled *secondary* members as regards the history of descent. Priority of morphological importance for comparative purposes is habitually conceded to those parts which are of earliest date and of most constant occurrence; accordingly the priority must here be given, not to the vegetative parts of vascular plants, though these appear first in the development of the individual, but to the spore-producing members, the sporogenous cells of which are believed to represent that tissue which formed originally the whole constituent mass of the sporophyte.

Having thus stated broadly the point of view which will be maintained throughout this memoir, it will be well to look back upon earlier opinions as to the morphological "dignity" of the sporangium. The earlier expressions of opinion on the nature of sporangia related to the pollen-sacs and ovules of the higher plants, these being very readily observed. It has been the misfortune of the morphological branch of our science that it was hampered by the early possession of a fairly accurate knowledge of the higher forms and recognition of their parts; as the result, a definite terminology, as well as a certain attitude of mind regarding them, became fixed at a date prior to the investigation of the lower forms; every one now would admit that the morphology of the higher plants is to be read in the light of a knowledge of the lower types, and yet morphologists commonly retain such views as would never have gained acceptance, if the course of investigation had been inverted, and the history of the progress of the science had led from the examination of the lower forms to that of the higher. On the most fundamental ideas of the relation of the sporangium to the vegetative organs, the views commonly held are incompatible with the probable history of descent; such views are to be looked upon as a legacy left behind by those so placed in the history of the science that their progress in morphological study was downwards along the branches of the developmental tree, instead of upwards.

The first expression of opinion on the morphological nature of sporangia appears to have been that of WOLFF, and naturally relates to the higher plants. He states his view that "even the seeds, notwithstanding that at first sight they have not the slightest resemblance to leaves, are still in fact simply coalescent leaves,"* and again he concludes "that the stamens also are in their nature simply leaves. In one word, in the whole plant, whose parts at first sight appear so excessively diverse, we see, on mature consideration, nothing more than leaves and stem, since the root belongs to the latter."† From these quotations it appears that WOLFF, though thoroughly acquainted with the parts of the flower, did not distinguish sporangia as a separate category, but as modifications of leaves or parts of leaves.

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* The question as to the sporogenous cells of modern sporangia being the lineal descendants, or, in other words, the morphological representatives of the sporogenous cells of a simple undifferentiated sporophyte will be discussed below, in the light of facts to be described later; at present, the view that in most cases they are so, may be taken as a working hypothesis strongly supported on general grounds.

The same was essentially GOETHE's view, arrived at by a distinct course of reasoning. GOETHE‡ (1790) at the outset drew attention to the fact that certain exterior parts of plants sometimes "change and pass into the form of adjacent parts either wholly or in greater or less degree." Of this change or "metamorphosis" he distinguishes three kinds, *regular, irregular, and occasional;* the third, since it includes only monstrous developments, may be at once dismissed. Under *regular or progressive metamorphosis* GOETHE included the changes involved in the development of the individual; the series, cotyledons, foliage leaves, bracts, and floral organs in an annual plant serve as an illustration. As *irregular or retrogressive metamorphosis* he designated such cases as the petaloid development of stamens, where parts which stand higher in the progressive series take, as they develop, the characters of a lower grade. In the recapitulation paragraphs, 115, 119, GOETHE sums up that, whether forming shoots, flowers, or fruits, it is still but the same organs which, under different names and various forms, answer the demands of nature ; all are referable to one, viz., the leaf.

It is plain, from the expressions used by WOLFF and GOETHE, that the idea of the sporangium as an independent member was not yet suggested ; the *pollen-sac* is regarded by GOETHE as the result of contraction of the margin of the staminal leaf (§47, p. 33) ; in writing of the ovules, he compares them with buds, and finally concludes (§93) that "the seeds, which differ from buds by being enclosed, and from gemmæ by the visible cause of their formation and separation, are still nearly related to both." Thus, notwithstanding that there was as yet no definite conception of the sporangium as an independent member, the theory of metamorphosis is intimately connected with the early views as to the nature of the sporangium ; it is to be remembered that the early writers on this subject, and especially GOETHE, had as yet no clear ideas as to descent, but had rather a bias towards a belief in the fixity of species; their conclusions are drawn from the study of the individual, not from a comparative study of plants at large; nor can we wonder that this should have been so at a time when the lower forms were hardly studied at all. As we proceed it will be shown how this morphology, based on ontogeny, has left permanent and erroneous traces, which the modern views of phylogeny have not yet obliterated; and that in certain most essential points the two methods are at variance—in which case, views based on sound comparison must take precedence over conclusions drawn from the mere study of the individual.

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* WOLFF, "De Formatione Intestinorum," 'Novi Comment. Acad. Petropol,' Tom. 12, 1766-1767, p. 405.

† *Loc. cit.*, p. 406.

‡ GOETHE's 'Werke.' SPEMANN. Berlin, vol. 33, p. 19, &c.

During the fifty years which followed the publication of GOETHE's essay, little was done to advance comparative morphology; the area of facts relating to the Phanerogams was extended, but in the light of our present knowledge it is plain that these could not be properly understood except upon a basis of comparison with the archegoniate plants. This is amply illustrated in the text-books of the period; in the concluding pages of the first volume of his 'Organographie Végétale,' AUG.-PYR. DE CANDOLLE (1827) re-asserts GOETHE's conclusions, though with a wealth of fresh illustration; the sporangium is still an unrecognised part, and the members of the whole plant, including the parts of the flower, are referred to the three categories of Root, Stem, and Leaf. While earlier writers hardly attempt a comparison with Cryptogams, TREVIRANUS did so ('Physiologie der Gewächse' (1838), vol. 2, p. 461, &c.), but in the absence of knowledge of the life-cycle in such plants, the result was not satisfactory. A more successful comparison was however made by VON MOHL in a Dissertation published in 1837;* his main conclusion was that in all the Vascular Cryptogams examined, the structure of the sporangium shows an undeniable similarity to the theca of an anther. But as a basis for clearer views two things were necessary, a knowledge of the life-cycle of the higher Cryptogams, and of the development of the flower, and of its parts in the Phanerogams.

The latter of these subjects, though earlier investigated by WOLFF, was taken up with vigour by SCHLEIDEN, and his results were embodied in his 'Grundzüge der Wissenschaftlichen Botanik' (1845), a book which had a profound effect upon the progress of morphology. We there find (p. 282) the comparison between the stamens of Phanerogams, and the sporophylls of Vascular Cryptogams broadly stated; the pollen-sacs and sporangia, and the pollen-grains and spores are also regarded as homologous; the view is maintained that the stamen is of foliar nature, but instead of assuming a progessive metamorphosis, and stating, as previous writers had done, that the stamen is an altered *foliage* leaf, SCHLEIDEN, resting upon the sure basis of development, did not go further than to admit that the stamen is of modified foliar nature (p. 284, &c.). In the absence of a theory of descent, this is, doubtless, the furthest he could safely go, and it will be seen that he there approaches nearer to the views to be put forward in this paper, than most of the writers who followed him.

While thus drawing comparisons between the sporangia of the Vascular Cryptogams and the pollen-sacs, and recognizing the stamen as of foliar nature, the writers previous to 1850 seem to have been content to place the ovule in a separate category; from GOETHE's time onwards it had been regarded by most botanists as the equivalent of a bud, but this is not surprising when we consider the peculiar form and structure of the ovule, which differs so widely from typical sporangia. It was only through the study of the life-cycle of the Vascular Cryptogams and Gymnosperms, and comparison of the latter with the heterosporous forms of the former, that the true nature of the ovule could be approached. This work was accomplished by HOFMEISTER in his 'Vergleichende Untersuchungen,' 1851, and those results of his labours, which at present chiefly interest us, were the establishment of clear views on alternation of generations, and the recognition of the homology of the ovule of Phanerogams with the megasporangium of the heterosporous Pteridophyta. From this time the ovule had to be viewed as bearing the same relation to the pollen-sac as the megasporangium to the microsporangium. Shortly after the publication of HOFMEISTER's discoveries, the 'Origin of Species' appeared (1859), but it seems at first to have affected the discussions on morphology only to a slight degree. The acceptance of a theory of descent, together with an adequate knowledge of alternation, should have led quickly to the establishment of the sporangia as forming a distinct category of members; but this result was long deferred, and for fully twenty years the questions discussed related as before to the "morphological dignity" of the pollen-sac, and of the ovule; little difficulty was felt by certain authors in assigning the pollen-sacs to a different morphological category from the ovules; many even held that the ovule might have a different morphological character in different cases. SACHS ('Lehrbuch,' 4th ed., p. 482), after describing the various positions of the ovules, writes: "If we apply general morphological definitions to these relations we should in the first of the above cases have ovules of an axile nature, they would be mere metamorphosed caulomes; where they arise below the apex of the floral axis, they would be regarded as metamorphosed leaves; where they arise laterally out of the margins of the carpels they would be viewed as metamorphosed pinnæ; for those which spring from the surface of the carpels there is no clear analogy with purely vegetative structure, but we may here remember the sporangia of the Lycopodiaceæ; further, it even seems possible to regard many ovules, *e.g.*, those of the Orchideæ, as metamorphosed trichomes, as in the case of the sporangia of Ferns and Rhizocarps." Some also held a similar view for the pollen-sac, asserting that while most stamens represent whole leaves, others are the result of metamorphosis of the axis itself (see EICHLER, 'Blüthendiagramme,' p. 47). It will be unnecessary here to follow out the controversies on these matters into their details; the position arrived at by those who admitted these divers morphological characters was, doubtless, due partly to the influence of GOETHE, and of his theory of metamorphosis, partly to the effect of SCHLEIDEN's insistence on the importance of the study of development of the individual in the solution of questions in morphology. Thus, the sporangium, whether it were that of a Vascular Cryptogam, or the pollen-sac or the ovule of a Phanerogam, was still considered as being borne by, or the morphological equivalent of, some vegetative organ, according as it was found to be comparable to one or another of these, as regards its position, and mode of origin.*

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* 'Vermischte Schriften,' 1837, p. 94.

This method of morphology takes into account the individual development; it rests on observations of ontogeny, but leaves out of account the opinions as to descent. It was not likely that such a method should long stand unassailed after evolution had come to be accepted. Though ALEX. BRAUN had already ascribed to the ovule the uniform character of a bud, it was STRASBURGER who appears first to have approached the question of variable morphological value of stamens and ovules from a general point of view.† He lays down at once the principle that "it is the highest problem of morphology to explain the form of plants, but this problem can only be solved genealogically." Having thus made descent the foundation for his morphology, he pointed to the general uniformity of construction of ovules, and expressed the opinion that from the phylogenetic aspect it is not to be imagined that such organs could have been formed at different times, and in different ways. He held that they were formed once only, among Phanerogamic plants, and have but one morphological character, viz., that of a bud, of which the nucellus is the axis and the integuments leaves. This opinion was shared by EICHLER,‡ who also on the grounds of descent, believed that such a structure as the ovule must have throughout the same morphological character; he too regarded it as a bud, assenting thereby to the position originally taken up by GOETHE. It was, however, a decided advance to have introduced the idea of descent into the argument, and to have dismissed the views of variable morphological character of the sporangia; but STRASBURGER did not follow his views out to their logical conclusion; the ovule, which is a megasporangium, is recognized by him as a bud; it corresponds to the megasporangium of heterosporous Vascular Cryptogams; are they also metamorphosed buds? The megasporangium and microsporangium of such forms are believed to have originated by differentiation of a uniform type of sporangium, are then all sporangia buds? Even the pollen-sac is a sporangium; is then a pollen-sac a bud? In order to be consistent this should be the interpretation of it by those believers in descent who also hold that the ovule is a bud. Evidently STRASBURGER when writing his great work on the Coniferæ and Gnetaceæ was still imbued with the old idea of metamorphosis; he still spoke of the three fundamental structures (p. 441), and obviously looked upon the sporangia of the higher plants as the result of metamorphosis of parts typically vegetative. It remained for GOEBEL to take the next step towards placing the morphology of the sporangium on a sound basis: rejecting the view which had been held all along, from the times of WOLFF and GOETHE, that in one form or another, the sporangium is the result of metamorphosis of some part of the vegetative system, he plainly stated that the sporangium is not referable in its origin to any other category of members. "As a shoot remains a shoot, and does not lose its morphological value (dignity) whether it arise as a lateral shoot on the growing point of a stem, or from the embryonic tissue of a foliage leaf (as in many Ferns), or is adventitious on a root, &c., so also a sporangium remains a sporangium and nothing else, whatever its position; sporangia are just as much organs *sui generis* as are shoots, roots, &c."*

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* SACHS, in his 'Lehrbuch,' 4th ed., which may be taken as fairly representing the spirit of the time of its publication (1874), makes the general statement (p. 153) that "every organ is either a stem (axis), or leaf, or root, or hair." But it is especially remarked later (p. 155) by way of limitation, that "the statement," *e.g.*, that "the sporangia of Ferns are trichomes, only means that they arise, like all hairs, from epidermal cells; hairs and Fern sporangia are in this respect morphologically equivalent." Morphological equivalence is, in this sense, simply equivalence of development in the individual; origin, by descent, is not taken into account in determining it.

† 'Coniferen und Gnetaceen,' p. 396, &c.

‡ 'Blüthendiagramme,' p. 45.

The above conclusion opened a new page in the history of the morphology of the sporophyte; a position was thus attained which, for the first time, became intelligible from the point of view of descent. Spore-production having been, as we must believe, a constantly recurring event during the whole course of evolution, and having preceded the vegetative development of the sporophyte, it was not possible to understand how the organs in which spore-production took place, could be merely the result of metamorphosis of those vegetative parts which, on grounds of phylogeny, there is every reason to believe were of later origin. By rejecting the old opinions, and recognizing the sporangium as an independent member, the way was at last cleared for a morphology based upon, or at least in harmony with, the conclusions as to descent, not upon the mere study of the development of the individual.

The question as to the relative importance of observations of the ontogeny, and conclusions as to phylogeny, is one of the most critical in all morphology, for on it depends the whole basis of the system: provided the conclusions as to phylogeny be sound, they should, in my opinion, have the precedence. But in practice it has been customary to hold the reverse, and to take the development of the individual as the basis of morphological treatment, while such views on descent as are based on comparison are often left practically out of account, or given only a secondary place. It will be useful to dwell upon this point so that readers may enter upon the subsequent discussion with an open mind.

From the time of GOETHE, observations of the development of the individual have had a strong influence upon morphological speculation. His introduction of the terms progressive and retrogressive metamorphosis, though they had at the time no clear meaning as to descent, doubtless gave a bias in a certain direction. SCHLEIDEN'S insistence on the importance of developmental data turned the current of observation into that direction. When evolution came to be recognized, and the embryology of animals was found to justify for them the acceptance of the recapitulation theory, GOETHE'S views were read in a new light, and the successive phases of the individual life of the plant also naturally appeared to illustrate, in a measure, the history of its descent; accordingly, speaking at present only of the sporophyte of the higher plants, the cotyledons might be viewed as the earliest type of leaf, the foliage leaves the next, and finally, the floral leaves and sporophylls. Any case of mere vegetative development of a sporophyll would be described, almost in the words of GOETHE, as a sample of retrogressive metamorphosis, or in the language of descent, as a reversion.

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* 'Bot. Zeit.,' 1881, p. 701.

A different position was taken up by the adherents of what has been termed the "differentiation theory";* for them the various forms of leaf are the result of differentiation of an original type: it was found that in their earliest developmental stages all leaves are virtually alike; here, it was maintained, might be recognized the fundamental form which underlies all the various lateral organs, while the development of these organs themselves was accepted as in fact a real metamorphosis, a differentiation to subserve various functions. The actual metamorphosis of one specialized organ into another was however denied; thus to the adherents of this theory stamens are by no means metamorphosed foliage leaves. GOEBEL, however, rightly points out "that such a metamorphosis of one form of leaf to another may occur," and cites his own experiments, by which leaves, normally developing into scale-leaves, were transformed in the course of their individual growth into foliage leaves.† He further cites those interesting cases of the appearance of sporangia on leaves of *Botrychium,* which are normally green expanded foliage leaves, noting that, where the sporangia occur, the vegetative development is reduced: similar observations on *Osmunda* and *Blechnum* are also quoted, and from these the conclusion was drawn that "the sporophylls are metamorphosed foliage leaves"; and still more explicitly it is stated for plants at large (*loc. cit.*, p. 118), "that the plant forms in the first instance leaves of only one type, the foliage leaves, though their growth is often modified by influences which appear in the course of development." But the facts do not necessarily bear out the interpretation thus put upon them: what is shown by such cases as that of *Botrychium,* or *Blechnum,* or *Osmunda,* is simply that a correlation exists between spore-production and vegetative development: where sporangia are present the vegetative growth is arrested, where sporangia are absent vegetative growth is more active: the further step that the sporophyll is a metamorphosed foliage leaf, and that the plant in the first instance forms only foliage leaves is an assumption, made in accordance with the custom of reading conclusions of phylogeny into the history of the individual, but without sufficient regard for wide-extended comparison. I do not admit that the priority of the foliage leaf in the development of the individual shows its priority in the history of descent: these observations of correlation do not appear to me to touch the question of priority of evolution.‡ I shall attempt to show on a basis of comparison of certain of the lower Vascular Cryptogams that, *in some cases at least,* foliage leaves may probably have been the result of sterilization of sporophylls, and I have little doubt that this mode of origin of foliage leaves has been a wide-spread one. I should be slow, however, to make a general statement that either the one or the other was the original form of leaf for all vascular plants, for the different lines of descent have probably been too divergent to allow of a simple statement covering all cases: and it seems possible that at least the primary leaves of the protocorm* may have originated in a different way from other foliage leaves.

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* HANSTEIN, 'Beitr. z. allg. Morph. d. Pflanzen,' 1882, &c.

† 'Bot. Zeit.,' 1880, p. 753, &c., also SCHENK's 'Handbuch,' vol. 3, p. 110.

‡ On this subject, compare 'Annals of Botany,' vol. 7, p. 373.

The idea of metamorphosis thus entertained by GOEBEL is primarily an *ontogenetic* one, but " it is extended by acceptance of the theory of descent."† In my view it has been customary to attach too great importance to observations of individual development, while too little attention has been devoted to broad comparison of the lower forms of the sporophyte, and to the phylogenetic conclusions which may be based upon such comparison; these should serve as a guide, as well as a check, upon the interpretation of the individual development. If the development of the individual be constituted the chief basis of the morphology of the sporophyte, while the check of more general comparison be only slightly applied, the conclusion may be arrived at that the first parts to appear were vegetative organs of simple type, then more complex vegetative organs, and that the spore-bearing members were of subsequent origin; it might also be concluded, with GOEBEL, that the sporophyll is a metamorphosed foliage leaf, or, in general terms, that spore-bearing members are the result of metamorphosis of pre-existent vegetative parts. But such a conclusion is plainly inconsistent with the story of the origin of the sporophyte, as it may be gathered from comparison of the lower archegoniate forms; for in them the production of spores is present *from the first*, and appears even to have preceded the simplest vegetative development. In such a case as this, where conclusions from the study of development are in antagonism to those derived from comparison, the former should, in my opinion, give way to the latter.

Moreover, the custom of reading the development of the individual as illustrating the phylogenetic history, is, at best, based only on experience of its truth in certain cases; because the epitome is found to be often true, it cannot be argued that it will be always true. In the rise of the sporophyte generation in archegoniate plants, I think we should hold, on grounds of broad comparison, that the development of the individual sporophyte cannot be taken *en bloc* as illustrating the history of the origin of the sporophyte at large. While spore-production appears to have been a constantly recurring fact from the first, comparison leads to the conclusion that the extensive vegetative phase which often precedes spore-production in the individual, was of more recent origin, appearing as an intercalated phase in the life-history. Accordingly it seems to me improbable that a sporophyll is really to be regarded phylogenetically as a metamorphosed foliage leaf; the converse would appear more reasonable.

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* Compare Treub, 'Buitenzorg, Annales,' vol. 8, p. 1 &c.

† *Loc. cit.*, p. 113.

The attempt must be made to formulate in the mind some idea of how the more complex forms of sporophyte came into being; such an attempt it is now proposed to make, and to arrive, primarily on the basis of general comparison, and in the second place on the ground of individual development, at some idea how the progression from the simpler to the more complex forms of sporophyte may have taken place.

In briefly stating the main problem certain views will, as already intimated, be assumed to be generally accepted; they are as follows:—

1. The homology of the sporophyte as a whole in such plants as show antithetic alternation.

2. The absence of any homology between the sporophyte and the gametophyte, or their parts.

3. The derivation of the sporophyte of vascular plants from some simpler form, more or less like that of the lower Bryophyta.

4. The recurrence of spore-production as a constant event in each life-cycle, during evolution of archegoniate forms.

5. That, other things being equal, an increase in the number of spores produced is an advantage.

It is believed that all the above theses would be upheld by botanists at large.

The main problem is to frame a reasonable theory of the mode of derivation of the simpler vascular plants, with foliar appendages, and discrete archesporia, from forms with no appendicular organs, and an undivided or concrete archesporium.

There are at least three imaginable ways in which the numerous isolated spore-producing parts characteristic of vascular plants may have originated from simpler ancestors with concrete archesporium:—

(1.) By subdivision or partitioning of an original concrete archesporium, and outgrowth of the isolated fragments, together with the tissue surrounding them; sterilization of a part of the sporogenous tissue might play an important part in bringing this about.*

(2.) By branching of a sporogonium (chorisis) and duplication of the head, as is seen in some monstrous Moss-sporogonia.

(3.) By a formation of entirely new archesporia at points where such were not present in forms believed to represent their ancestors; such archesporia would have no direct connection by descent with pre-existent ones, but might in our view of sterilization be recognized as reversions.

It has been one object of the enquiry detailed below to see if among the lower vascular plants evidence can be found of any, or of all of these processes.

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* It should here be remarked that the sub-division thus suggested may be further complicated by the continued apical or intercalary growth of the part concerned; and, as in the development of shoots and leaves, the increase in number of appendicular parts may be closely connected with such continued growth, so, I conceive, may also the number of spore-producing members. An application of this will be found at p. 534, &c.—F.O.B., February, 1894.

The great gulf between the Bryophyta and the Vascular Cryptogams must be faced sooner or later. It seems to me useless to turn away and say that the gulf is not to be bridged by hypotheses, and that the tracing of homologies in the sporophyte is hopeless, while our knowledge of the details of structure and development of those very forms which we believe to be near the boundary line is still so far from being complete. It is true that direct connecting links are almost absent; that fossils afford little help, and cannot be expected to yield much in the way of developmental data. But the world's surface has been almost completely over-run, without disclosing in recent years new forms which would obviously take an intermediate place, so that it would be idle to wait indefinitely for the discovery of new forms to help us in the solution of the difficulty. It, therefore, appears to me to be a duty to turn to the living vascular plants nearest to the border line, and endeavour, by careful comparative study of them, to add to the knowledge of their details, with a view to attaining a basis for a reasonable hypothesis.

In pursuing this investigation, it will be important to fix the attention on organisms lower in the scale rather than on the higher forms; for it is essential not to obscure the issues by irrelevant references to the parts of organisms higher in the scale, such parts being often described by names which bear preconceived ideas with them; accordingly, notwithstanding the attractions which such comparisons present, allusions to the Phanerogams will for the present be almost entirely omitted, and the application of the results obtained to the explanation of the forms of the higher plants will be deferred to a future occasion. The first step will accordingly be to briefly review such facts relating to the Algæ and Bryophyta as, being already in our possession, may have their bearing upon the main points of our enquiry.

STERILIZATION IN THE ALGÆ AND BRYOPHYTA.

Reference having been made above to the part played by sterilization in the development of the sporophyte in the Bryophyta, and its progressive steps being more obvious in those plants than elsewhere, it will be well to examine the facts already recognized in them, before proceeding to the study of the Vascular Cryptogams. There is good reason to believe that the latter were derived from some Algal-Bryophytic ancestry, so that observations of progressive elaboration in the Algæ and Bryophyta may be reasonably accepted as suggestive of similar progress in the course of evolution of vascular plants.

In the simplest plants showing antithetic alternation, viz., certain Confervoideæ, the zygote undergoes on germination a subdivision of its protoplasmic body into a number of parts; there is, however, no differentiation of these, all are alike capable of acting as carpospores, and producing new individuals. Differences may be recognized between different types as regards the presence or absence of cell-walls; thus, in *Oedogonium* or *Sphæroplea*, the carpospores may be primordial cells, while in

Coleochæte they have a definite cell-membrane; this is, however, promptly left behind by the escaping protoplasmic body. In these Algæ, the existence of the sporophyte is barely sketched out, and the parts of it show no differentiation; it is even an open question whether this rudimentary sporophyte of certain Algæ be truly comparable with that of the Bryophyta; but in any case it occupies the same position in the life-cycle.

Differentiation is, however, present even in the simplest Bryophytic forms, as in *Riccia glauca*, where the peripheral layer of cells constitutes a temporary wall round the undifferentiated mass of sporogenous cells within (comp. KIENITZ-GERLOFF, 'Bot. Zeit.,' 1874, Plate 3, figs. 1–6). Further steps in advancing complexity are illustrated in other Liverworts; these may involve (*a*) sterilization of the whole transverse thickness of tissue of the sporogonium, proceeding from the base upwards, or (*b*) in differentiation of cells of the potential sporogenous tissue which remains, and sterilization of certain of them. In the rare genus, *Oxymitra*, the sporogonium is virtually similar to that of *Riccia*, but the cells of the wall appear to be less regular and definite, while certain of the cells of the sporogenous inner mass remain sterile, but without undergoing any special development (LEITGEB, 'Lebermoose,' Heft 4, pp. 42–45, &c.). In *Corsinia*, also, such sterile cells are found, while here the complete sterilization of the lower part of the sporogonium shows a clear distinction of apex and base, which was absent in the earlier-named genera. In *Boschia*, the sterile cells among the spores take the elongated form, and spiral or annular thickening, appearing, when mature, as the well-known elaters. Thus, within the Riccieæ, both types of sterilization, (*a*) and (*b*), are initiated;* in the Marchantiaceæ these characters become more marked, the elaters especially being a prominent feature, and showing some regularity of arrangement.

As regards (*a*), the sterilization of the whole thickness of tissue of the sporogonium, this is found in *Marchantia* to involve the whole hypobasal half of the embryo, the result being a pad of sterile tissue of the foot; but in Jungermannieæ the hypobasal half remains small, while the epibasal half dividing into octants, each of these undergoes repeated transverse division and great elongation; all the lower part of the tissue thus produced is vegetative, while the spore-production is confined to one or two tiers of cells at the apex. Here, then, is extensive sterilization extending far upwards into the body of the sporogonium—an intercalation of an intermediate vegetative stage between the zygote and spore-production. In the remaining family, viz., the Anthoceroteæ, the case as regards the type (*a*) of sterilization appears very similar to that in the Marchantiaceæ, only the hypobasal portion of the embryo being completely sterile throughout the whole transverse section, and forming the enlarged haustorial foot.

Turning to the type of sterilization (*b*), viz., differentiation of the potential sporogenous tissue and sterilization of certain of the differentiated parts, we see considerable differences in the disposition of the sterile parts. In the simplest cases the sterile cells do not differ from early arrested spore-mother-cells (*Oxymitra*); or they may be elongated and specially thickened, as elaters; these may be arranged with no regularity (*Boschia*), or they may radiate from the basal limit of the capsule (*Marchantia*); or project almost horizontally inwards from the wall of the spherical head (*Jungermannia trichophylla*, HOFMEISTER, 'Higher Cryptog.,' Plate 9, fig. 33); or they may appear as vertical rods or trabeculæ passing from the outer wall to the base of the cavity (*Frullania dilatata*, HOFMEISTER, *loc. cit.*, Plate 12, fig. 9, or *Lejeunia serpyllifolia*, LEITGEB, *loc. cit.*, Heft 1, Plate 1, fig. 14).

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* It may be a question whether the genera of Algæ and Liverworts quoted really illustrate their phylogenetic origin.

In the examples hitherto cited there is no association of the sterile elaters in masses; this is seen to occur, however, in various genera, and with interesting differences of detail. HOFMEISTER ('Higher Cryptog.,' p. 38), in describing the head of the sporogonium of *Pellia epiphylla*, remarks that "a whole string of cells lying in the longitudinal axis of the young fruit assumes this spindle form; around this string the rest of the cells destined to form elaters are arranged, radiating upwards. LEITGEB ('Lebermoose,' Heft 3, p. 57) points out that this axile strand does not extend further than about two-thirds of the distance from the base upwards through the cavity of the capsule; he also recognizes that the strand consists of grouped elaters. In certain other genera (*Metzgeria* and *Aneura*) a somewhat similar arrangement is found, but in an inverted position. LEITGEB states (*loc. cit.*, p. 31) that in "*Metzgeria* a group of cells at the apex, situated in contact with the wall of the capsule, is arrested in its growth without being transformed either into elaters or spore-mother-cells"; and, again, on p. 40, "the rows of spore-mother-cells and elaters do not converge to a point at the apex, but to a group of cells below it, composed of cubical cells, and there is no doubt that these correspond to the original internal cells of the upper storey of the spore-producing space." In *Aneura** also a somewhat similar central sterile mass is found attached to the wall at the apex of the sporogonium, and extending for a distance down into the spore-cavity as a solid column, but finally branching off into numerous separate elaters. In *Aneura pinguis* the relatively large sporogonium has a well-defined columella of sufficient size to be easily seen with the naked eye, and extending two-thirds down the cavity of the sporogonium: in *Aneura multifida* the sporogonium is smaller, and the columella is represented only as a minute mass of cells, projecting downwards about one-eighth of the distance through the cavity: from these incomplete columella-like masses the elaters radiate downwards into the mass of spores. The transition from the parenchymatous cells of the columella to typical, spindle-shaped, spirally-thickened elaters is beautifully illustrated in *A. multifida*, and may also be traced, though not with the same completeness, in *A. pinguis*. In these sporogonia also it would appear that the columella is the result of massing together of sterile elaters, and it is to be noted not only that the columella is larger and more complete in the species having the larger sporogonium (*A. pinguis*), but also that the columella is more elaborate here than in the examples previously quoted.*

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* I am indebted to Professor FARMER for sections illustrating these points in *Aneura*, and for drawing my attention to them.

These very interesting cases of apparent grouping of the elaters to form a solid sterile axile strand, extending part way through the cavity, or even a sterile mass of ordinary cells, not developed as elaters, depending from the apex, appear to me to illustrate a matter of some importance. I think we may recognize in them imperfect steps towards the formation of a complete columella in the centre of the capsule, and see therein illustrated how, by the collection of sterile cells, isolated and uniformly diffused in other types, into a central position, a solid column of such tissue may be the result; such columns are here incomplete, but they suffice to suggest a possible mode of advance in sterilization, and it will be seen that this idea had not escaped the mind of LEITGEB.

In the Anthoceroteæ the sporogonium attains a greater complexity than in other Hepaticæ, but it is not uniform in the different genera, and the variations in structure have made them the subject of a careful discussion by LEITGEB ('Lebermoose,' Heft 5), from which the following facts and quotations are extracted.

In the more complex genera, *Anthoceros* and *Dendroceros*, the lower part of the sporogonium is developed as a foot, which keeps up physiological connection with the gametophyte; there is no seta, but the whole of the upper part of the sporogonium is composed of a columella, round which, and arched like a dome over its extreme apex, is the sporogenous layer, while the sporogonial wall, of several layers, covers this externally. The central cells, formed by periclinal division from each transverse tier of four in the young embryo, are entirely converted into the columella, the sporogenous layer being cut off from the outer cells by their first periclinal division. But of the sporogenous layer itself the majority of cells are sterile, while only the minority produce spores; the sterile cells in many species form a connected network, in the meshes of which the spore-mother-cells lie (*loc. cit.*, p. 6). The intercalary growth at the base of the sporogonium is apparently unlimited.

In the genus *Notothylas* not only are the characters different from the above, but there is also a most interesting variation in structure within the genus itself. The intercalary growth appears to be limited, when the limit occurs early, dwarf capsules, which are found in all species, are the result; sometimes, however, the growth is long continued. In certain species some of the capsules are like those of *Anthoceros* as regards the columella; but "in all species of *Notothylas* capsules are found, in which a columella is present it is true, but the cells of the columella are quite similarly formed to the other sterile cells of the capsule-cavity, and are very easily separable. Investigation of such capsules shows that the columella is not formed independently as in *Anthoceros,* and " separately from the spore-bearing layers, but arises by secondary differentiation within the spore-bearing space, and thus coincides in this respect with the columella of the Moss-capsule" (LEITGEB, 'Lebermoose,' vol. 5, p. 7). "But in some species of *Notothylas* (perhaps in all ?), there are also capsules in which the columella is absent from the first; the sterile cells together form a connected tissue, a network which uniformly fills the whole cavity of the capsule . . . It is instructive that such capsules differ only by gradual steps from these with a columella which have just been described." . . . "By the formation of such columella-less capsules *Notothylas* is directly connected with other Liverworts." (LEITGEB, *loc. cit.,* vol. 5, p. 8.)

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* This genus has already been treated by LECLERC DE SABLON ('Ann. Sci. Nat.,' 7th Series, vol. 2, p. 161), and excellent figures given, illustrating the structure of the columella (Plate 11, fig. 46). He also gives details of various other Liverworts; those relating to Frullania will most claim our attention (see below, p. 557).

"If now, as I have endeavoured to show as probable, *Notothylas* be regarded as a form related to the Jungermanniaceæ, this must clearly be the case also for all the Anthoceroteæ, which are directly allied with *Notothylas,* and are doubtless descended from a similar form. The sterile cells at first uniformly distributed through the whole spore-cavity, though connected together, first united at the axis of the capsule to form a strand of cells the elements of which were not as yet different from the rest of the sterile cells. As above noted, such capsules are still found in *Notothylas.* Probably the next step was that the mode of development of the cells composing the axile strand differed from that of the cells outside, in the spore-cavity. Probably this form also is present in *Notothylas,* and I refer to the capsules described above which show a development of the columella similar to that of *Anthoceros.*" (LEITGEB, *loc. cit.,* p. 10.)

In the passages thus quoted, LEITGEB's view of the progression of sterilization in the Anthoceroteæ is quite plainly stated; he distinctly recognizes the association of sterile cells together to form sterile masses as exemplified by the columella; similar though less complete examples have been above cited in *Pellia, Aneura,* and *Metzgeria,* and we shall conclude that such association has been a feature in the advance of structure of the sporogonia in various genera of Hepaticæ.

There is one further point as regards the Anthoceroteæ which will be of theoretical interest: of the products of the sporogenous layer the majority of cells are sterile. Now it is quite possible and conceivable, after what has been noted above, that these sterile cells might further be associated together to form septa, which would thus partition off the sporogenous cells into separate compartments. We have no example of this among Bryophyta, but it would be the next natural step in continuation of the sterilizing process above traced.

The Mosses present fewer points of interest in this connection; a certain parallelism may be traced with what has been described above—a progression of complexity from the simpler types of Phascaceæ to the Bryineæ; and again it may be noted that whereas the archesporium in *Sphagnum* is of a closed dome-like form, that of the Bryineæ is like a barrel open at the ends, and it may be suggested that this latter condition is the result of sterilization of the apical part. But in the Mosses the whole sporogenous layer bears spores; sterile cells appear to be absent from it, and if the potentialities of further development of those sterile cells be such as have been suggested in the previous paragraphs, then such potentialities will not have a place among the present living Mosses. From a theoretical point of view, however, the differences in place of origin of the archesporium are important; in *Sphagnum* it is derived from the amphithecium, in most Mosses it originates from the endothecium, and a similar difference of detail being also seen in the *Anthocerotecæ*, we have good reason to conclude that the actual layer which gives rise to the archesporium is not to be strictly defined for all Bryophyta, we shall thus be prepared to think it possible that the spore-production might be relegated to still more superficial positions in other plants, as is actually the case in the Vascular Cryptogams.

The elaboration of form of the capsules of some Mosses is interesting, as showing organisms making the best of a type of construction which is essentially unfitted for carrying on assimilation on a considerable scale. The whole sporogonium of *Anthoceros* is green, and can assimilate, though in most Liverworts assimilation is carried on only in a minor degree in the sporogonium, or not at all; and even in *Anthoceros* there is no specialization of form, and little specialization of structure to this end. In certain Mosses, however, there is more specialized structure: the seta usually contains little chlorophyll, but the head of the sporogonium, and especially the outgrowth of the apophysis where present, is the part in which assimilation is most active. The development of the apophysis for this purpose reaches its highest type in *Splachnum luteum* (compare VAIZEY, 'Annals of Botany,' 5, p. 1), in which it appears as an expanded disc, bearing numerous stomata, and filled internally with spongy chlorophyll-containing parenchyma. This is the most elaborate type of construction for assimilating purposes seen in the sporophyte of Bryophyta, and it is clearly the result of a comparatively slight modification of parts, already sterile, of the ordinary type of sporogonium.

In the above paragraphs some of the main phenomena of advance in the sporogonium of the Bryophyta have been briefly described, and it seems probable that progressive sterilization of sporogonous cells and progress of complexity of the sporogonium have gone hand in hand. As we recognize that vascular plants probably originated from some Algal-Bryophytic ancestry, it will be useful to carry forward to the study of the former clear ideas of the modifications which appear to have played a part in the advance of the Bryophyta. It is possible that there may be no homologies, possibly only slight analogies, but we should at least prepare ourselves to appreciate them if they exist.

The comparative study of the sporophyte of the Bryophyta leads to conclusions which may be formulated as follows:—

I. There is evidence of the sterilization of potential sporogenous cells, and the first result was probably the formation of a protective peripheral wall (*Riccia*).

II. In the space within this wall other sterile cells may be dispersed among the sporogenous cells (elaters, &c.).

III. Sterile cells similar to those thus isolated may in some forms be grouped together, producing coherent sterile masses of tissue (columella of *Pellia*, *Metzgeria*, *Aneura*, and Anthocerotеæ).

IV. In all the more complex forms a central sterile columella exists, while the spores originate from a definite band outside it (the archesporium).

V. The position of this band is not constant, originating sometimes more deeply, at other times being nearer the surface.

VI. The archesporium may give rise to both sterile and fertile cells (*Anthoceros*).

VII. In the lower part of the sporogonium a complete sterilization of the whole thickness of the sporogonium may be seen. This involves, first, the hypobasal half of the embryo, as in Marchantiaceæ; or, progressing to successively higher tiers of cells in the epibasal half, forms the sterile seta of the Jungermannieæ.

VIII. Intercalary growth may play a prominent part both in the sterile (*Jungermannia*) and in the fertile parts (*Anthoceros*).

IX. Elaboration of external form is suggested (*Polytrichum*, *Splachnum*), but never carried far.

X. Assimilation may be actively pursued in the sterile tissues, either in those of the seta (including the apophysis, *Splachnum*, &c.), or in the fertile part of the sporogonium (capsule of *Anthoceros* and most Mosses).

XI. Differentiation of tissues is fairly advanced in the seta of some Mosses.

Now under the above heads are included those features which, if collectively present in one organism, might lead to the production of such more elaborate forms of shoot as are seen in the lower vascular plants, except two, and they are prominent ones, viz.:—

I. The formation of appendicular organs.

II. The subdivision of the archesporial layer to form isolated patches, instead of one continuous tissue.

With regard to the former—the origin of appendicular organs—we are still in the dark, though various suggestions have been made. In approaching this difficult question, I wish it to be understood that the criticisms and suggestions now to be made are offered only in the most tentative way, while it will remain to be seen how far they may be supported by the developmental facts to be described below.

Most of the hypotheses hitherto advanced have been based upon the belief that it is in the Filicineous series that the nearest point of contact between living Vascular Cryptogams and Bryophyta is to be found. For instance, KIENITZ-GERLOFF (' Bot. Zeit.,' 1878, p. 55), in putting forward his suggestion that the head of the

Moss-sporogonium is foliar in its nature, while the axis is rudimentary and is represented only by one quadrant of the upper half of the zygote, which later takes part in the formation of the foot, draws his detailed comparison with the Fern-leaf (pp. 55–56). Again, PRANTL ('Unters. z. Morph. d. Gefässkrypt.,' Heft 1, p. 62, &c.) discussed the matter from the point of view of a comparison between Moss-fruits and the simplest imaginable Fern plant. LEITGEB was, however, more cautious (*loc. cit.*, Heft 6, p. 61), though he seems to have had comparatively large-leaved forms in his mind when he wrote as follows:—"I believe that this much is certain: if we would trace the spore-forming generation of the Vascular Cryptogams from Liverwort-sporogonia, we must designate the cotyledons as the homologues of the latter, upon which at first the spore-formation must have been carried out, until, when the embryonic branching, *i.e.*, the formation of the stem and its lateral members (leaves) took place, it passed over to the latter."

Very much the same view was entertained by NAEGELI ('Abstammungslehre,' p. 476). Starting from the consideration of the steps of advance of the sporogonium of Liverworts, and distinction of a vegetative base from the sporogonial head, he discussed the mode of elaboration of the latter, suggesting it as possible that the apex became vegetative, "and that the sporogonium developed as a lateral outgrowth on the apex; further that this sporogonium by further modification . . . . developed into the leaf-bearing stem." But he contemplated it also as possible "that the thallome-like sporogonium, as it became vegetative, may have extended directly (without a preliminary lateral branching) to the leafy stem." He further recalls the fact that branching occasionally occurs in Moss-sporogonia, and suggests that this may have recurred repeatedly, in connection with continued apical growth of the whole. "With the continued growth of the sporogonium in length, the spore-producing portion of it behind the apex is raised aloft, so that a stalked sporogonium is the result. The lateral branches are also fertile, and develop as sessile sporogonia. Thus a strobiloid sporogonial system arises which is either the direct continuation of the original thalloid body, or if, as was first assumed, a lateral sporogonium was produced by branching, a lateral continuation of it" (p. 477). He then suggests how the sporogonia may have increased in size, and partially passed over to the vegetative state, their main body becoming leaf-like, while the spore-production is limited to a part of them: the result would be a leafy axis, of which all the leaves would be sporophylls, a condition not unlike that of *Lycopodium*. The idea of NAEGELI (as embodied in his 'Abstammungslehre,' pp. 475–479) refers the elaboration of the sporogonium so as to form the leafy shoot to some form of *branching*: in this it does not differ from the other theories above referred to; in all of them the origin of foliar members has been imagined as some process comparable to such branching of sporogonia, as is sometimes seen in abnormal cases. *In all of them the apex of a sporophyll is assumed to represent the apex of a sporogonium, or of some branch of a sporogonium.* I think that the origin of this idea is to be found in the assumption so often made that the nearest point of contact with the Bryophyta is to be sought among the Ferns. Now the Filicineous leaf, even in its simplest forms, is a highly organized foliar structure: in many ways the leaves of Ferns are peculiar, while in their higher developments they attain such complexity as is hardly equalled in the vegetable kingdom. It appears to me improbable that even the simpler types of the Filicineous leaf will serve as indications of the origin of the foliar development exhibited in other vascular plants. I think it is rather among those series of homosporous Pteridophyta, such as the Lycopodineæ and Equisetineæ, in which a simpler type of leaf is the rule, that the inquiry may be pursued with better prospect of success.

Now the Lycopodineæ and Equisetineæ are *strobiloid* types, in which the vegetative leaves and sporophylls are relatively small, and the axis relatively large; while the leaves are closely associated together in large numbers on the axis. The sporophylls usually bear but few sporangia, and neither vegetative leaves nor sporophylls show localized or continued apical growth in any marked degree. It has become the practice in recent years to treat the shoot—whether sterile or fertile—as a whole (SACHS 'Lectures,' p. 3), of which the axis and leaves are component parts. This thoroughly sound practice is more obviously advantageous in cases where the axis is relatively large, and the leaves relatively small and crowded, and it will assist us in our discussion of these strobiloid Pteridophyta.

The theories of origin of foliar members above cited, except perhaps NAEGELI'S, assumed that the apex of the sporogonium represents the apex of the coming sporophyll, while the axis originated either as a somewhat similar branch, or as a lateral bud in some way not always strictly defined. As the result of comparative study of Bryophyta and Vascular Cryptogams, I would now put forward as a working hypothesis, *that in the strobiloid Pteridophyta the apex of the sporogonium is the correlative of the apex of the strobilus.* The result of this would be that *the appendicular organs would all have been of lateral origin,* appearing as an eruption of outgrowths, probably unimportant at first, from the surface of the relatively preponderating axis. Such branching of the sporogonium as occasionally is seen would find its correlative, not in the formation of leaves, but in the terminal branching of the shoot or strobilus, as in *Lycopodium*, or rarely in the strobilus of *Equisetum* ("acrogene Verzweigung," NAEGELI, 1, *loc. cit.*, p. 478). As in the higher Bryophyta, so in the strobiloid Pteridophyta, a distinction is commonly found between vegetative and spore-bearing regions of the sporophyte; the seta of the former may then be the correlative of the vegetative region of the latter, while *the sporogonial head would correspond to the whole strobilus.*

It would be premature to discuss details of origin of the appendicular organs, but on the view above sketched, it would appear possible that these should originate, not only from the sporogonial head (as sporophylls), but also from the sterile region (as vegetative leaves), and these two types of foliar organs may have been produced independently of one another, while a further addition to the vegetative region might be made by sterilization of sporophylls. (See below, p. 535, &c.)

I only know of one previous suggestion of such a nature as the above; it was made by the late Mr. VAIZEY, in a very tentative way ('Roy. Soc. Proc.,' vol. 45, p. 151), in connection with his work on the apophysis of *Splachnum luteum.* He wrote as follows: "That the apophysis performs the functions of a leaf, and is, therefore, *analogous* with the leaves of vascular plants, I think there can now be no doubt, and as this structure is a development of the sporophyte, the possibility of its being also *homologous*, either directly or indirectly, suggests itself. I am myself inclined to believe that the two are homologous." While admitting the analogy thus brought forward, I am not prepared to contend for the actual homology of the apophysis with a leaf or leaf-sheath. But I think we should do wrongly if we neglect to recognize that there is here, at least, a suggestion how a foliar development such as that of *Equisetum* may have taken its origin. If such sheaths were produced in large numbers in the lower vegetative region of a sporogonium, something like the simple shoot of *Equisetum* might be the result. A similar development in the sporogonial head might produce the strobilus. This view would harmonize readily with the embryology of *Equisetum* as described by SADEBECK, 'Pringsh. Jahrb.,' vol. 11; and by BUCHTIEN 'Bibliotheca Botanica,' No. 8, 1887.

But such development as this would involve the second prominent feature which we above noted aswanting among the Bryophyta (above, p. 491), viz., (2) the subdivision of the archesporial layer to form isolated patches, instead of one continuous tissue. Is there any reason to think such a subdivision probable, and how could it take place? To answer this question recourse must be had to comparison of certain details of spore-production in the Bryophyta, and in the Vascular Cryptogams; the former are already provided by the researches of LEITGEB, while I hope to add to the latter in subsequent pages. The full discussion of this subject must, therefore, come at the end of this memoir; but in the meanwhile certain facts and conclusions from study of the Bryophyta may be considered. It has been seen that sterile cells (elaters) in certain Liverworts appear to be massed together, and form solid tissues, as in the case of the columella; it is, therefore, reasonable to expect that some similar process may occur again in such Liverworts, or other plants, as show sterile cells scattered through their sporogenous masses. Now the *Anthocerotecæ* have by various writers been recognized as plants whose sporophyte approaches that of vascular plants more than that of other Bryophyta (LEITGEB, *loc. cit.*, Heft 6, p. 60; PRANTL, *loc. cit.*, Heft 1, p. 62). In these plants a large proportion of the cells produced from the archesporium are sterile, and it would thus appear that a formation of sterile septa might be expected to result from a process of massing of these, such as is shown by LEITGEB to have produced the columella. But while noting this, I would not be understood to use it as more than an illustration, for I do not suppose that any living Bryophyte really represents the progenitors of vascular plants.

Thus we see that certain of the factors which might lead to the production of a more complex type of sporophyte are represented in living Bryophytes.

The next step will be, bearing these facts in mind, to inquire whether on the other side of the gulf, *i.e.*, among the lower vascular plants, characters of a similar nature are to be observed, and we shall look for evidence in answer to the following questions :—

(1.) Are sterile cells distributed among the sporogenous cells in any Vascular Cryptogams ?

(2.) Do any Vascular Cryptogams show a distinct part which may be correlated in position, structure, development, and function with the sporogonial head of the Bryophyta ?

(3.) Are the sporangia ever borne in such relation to one another as to suggest a common origin by sub-division of simpler parts ?

(4.) Is there direct evidence in any Vascular Cryptogams of conversion of potential sporogenous tissue into masses of sterile tissue, or conversely of conversion of sterile septa into spore-producing cells ?

I am quite aware that, even if all these questions were answered by abundant evidence in the affirmative, this would not afford complete proof of the mode of descent of Vascular Cryptogams from simpler Bryophytic forms. Few biological hypotheses are completely proved, or even susceptible of proof, under the present order of nature. But what I submit is, that the search for answers to such questions as the above may, in the light of the facts already derived from the study of the Bryophyta, go far to support the working hypothesis above sketched in its broad outlines, and raise it to the position of a reasonably probable theory.

EQUISETUM.

The first detailed account of the development of the strobilus and sporangia of *Equisetum* was given by HOFMEISTER for *E. arvense* ("Higher Cryptogamia," 'Ray Soc.,' p. 280, Pl. 36); his results were in the main adopted and verified by RUSSOW ('Vergl. Unters.,' p. 147, and Pl. 9), but, as regards the origin and early history of the sporangium, the investigations of the latter add little to the facts already acquired by HOFMEISTER. A point of difference between these two writers is in the reference of the sporangium, as regards its origin, to a single parent cell. HOFMEISTER speaks of the shields (sporangiophores) exhibiting "at five or six points a rapid cell-multiplication, produced by the division of one of the cells of the under surface of the shield," and he appears to refer the whole of each sporangium to *one* original cell. It will be seen that the essential part of the sporangium, viz., the sporogenous tissue, is referable in most cases with certainty to the successive segmentations of a single original cell, but the sporangium as a whole is of the eusporangiate type; this was recognized by RUSSOW, and does not now admit of any doubt.

The most accurate examination of the sporangiophores and sporangia of *Equisetum* hitherto made has been by GOEBEL, his illustrations being taken from *E. limosum* ('Bot. Zeit.,' 1880, p. 549, Pl. 8, figs. 2–6; also, 1881, Pl. 6, fig. 1). The two most important of these are quoted in his 'Grundzüge,' as fig. 223A and 223B (but under the name of *E. palustre*); in these figures, the archesporial cells are shaded so as to distinguish them. It has always been a difficulty to me to accept the story of development, as stated by GOEBEL; the earlier stage ('Bot. Zeit.,' 1881, Pl. 6, fig. 1, quoted as 'Grundzüge,' fig. 223A) shows an archesporium consisting of only one cell, which is covered externally by two relatively deep cells, one of which is superficial; the later stage (fig. 223B), shows the sporogenous cells, eight in number, covered at the apex by three relatively shallow cells, which do not together measure a greater depth than the one superficial cell of the earlier figure. Assuming the figures to be drawn under the same magnifying power (on which point I find no statement in the original paper, or in the 'Grundzüge'), it would seem either that the cells overlying the archesporium contract and become shallower as development proceeds, or that the recognition of the archesporium as a single cell in the earlier stage (fig. 223A) is at fault. Moreover, the history of development, as illustrated by the figures, is far from complete. In order to give a satisfactory account of so bulky a structure, it should be cut in three directions, radially, tangentially, and transversely, at different stages, but this was not done by GOEBEL. It thus appears that there is need of a re-examination of development of the sporangia of *Equisetum.*

Equisetum arvense L. (figs. 1–9).

The results yielded by a study of *E. arvense* have afforded a more complete account of the early phases of development than in other species, and they will be described first. *E. limosum* has also been examined for purposes of comparison with GOEBEL's results and with the data from *E. arvense.* It will be seen that the details in the latter species are liable to considerable variation, and differ in some points from the more regular *E. arvense.*

Radial sections through the very young strobilus of the last-named species show that the sporangiophores arise as already described by HOFMEISTER, RUSSOW, and GOEBEL; they appear as ring-like outgrowths, which, in the longitudinal section, involve a considerable number of cells, with a fan-like tracery. Comparing those of *E. arvense* (fig. 1) with those of *E. limosum* (see GOEBEL, 'Bot. Zeit.,' 1880, Plate 8, fig. 2), the former are of a more bulky character, and this will be found the case also with the sporangia of the species. As in *E. limosum,* the tissues of the sporangiophore, when cut in radial section, are referable to the outgrowth of six cells, but many more anticlinal divisions appear in these before the convex outgrowth is considerable, than is the case in *E. limosum* (compare GOEBEL, 'Bot. Zeit.,' 1880, Plate 8, fig. 2). Accordingly the sporangiophore of *E. arvense* is from the first of a more massive type than in *E. limosum.* In the larger sporangiophore shown in fig. 1 it is believed that the cells marked (⊙) are correctly recognized as those which will give rise to the essential parts of two sporangia; it will be observed that these cells occupy corresponding positions on either side of the sporangiophore, adjoining the anticlinals 1 and 5. As the sporangiophores grow older the anticlinals become more strongly curved, owing to the more active growth of the central parts, while the sporangiophores of successive series coming in contact press upon one another, and their sides become flattened. Growth of the future sporangia now becomes more rapid, so that they begin to project (fig. 2), while cell-divisions rapidly succeed one another. The succession and exact position of their walls is liable to some variation, as is almost always the case in the development of large cell-masses. The description now given is that which is found to be most typical, and it will be seen that a single cell is the ultimate parent of the essential parts of the sporangium; such a cell is shown, still undivided, in fig. 1, adjoining the anticlinal 5, in the larger sporangiophore. The first division in this cell is by a periclinal wall (fig. 1) separating an inner cell (shaded) from an outer one; the inner cell is divided first by anticlinal walls at right angles to one another (compare figs. 2, 3, and 7) into four, and subsequently by periclinal walls into eight cells, which form the lower part of the sporogenous tissue. But this is not the whole of the tissue from which spores are formed; a comparison of older stages (figs. 3, 4, 5, 6) shows that, by subdivision of the outer of the two original cells, shown in fig. 1, additions are made to the sporogenous tissue; these appear in the following way. The outer cell usually divides by crossed anticlinal walls (figs. 2, 3, 7, and 8), which are succeeded by periclinals (figs. 3, 7); the inner cells thus formed are added to the sporogenous tissue, while the outer form the apical part of the wall of the sporangium and the tapetum; a careful comparison of figs. 1–7 will show that the sporogenous tissue is not limited by the first periclinal wall, but that cells derived from part of the outer of the two original cells form an essential part of the sporogenous mass; these cells are marked with a cross (×) in all the figures. In order to obtain tangential sections, which shall traverse the axis of the obliquely placed sporangium, the direction of section must be slightly inclined; such a section is seen in fig. 7, in which the cell-tracery corresponds in all essential points to that of fig. 4; it further demonstrates how slight as yet is the projection of the individual sporangia beyond the margin of the sporangiophore, as is shown by the gentle curve of the surface above the apex of the sporangium.

Owing to this very slight projection of the young sporangium, and its oblique position, transverse sections are not easily obtained in the very young state; but when the sporangium has attained the size and development of fig. 6, a transverse section shows plainly enough the relations of its parts (fig. 9); the sporogenous tissue which is shaded is readily referable in its origin to the segmentation of a single cell of the transverse section; certain cells of the adjoining tissue develop of large size, and with dense protoplasmic contents, and it has been difficult to decide whether there be not also an addition to the sporogenous tissues from such lateral cells; some longitudinal sections appear to support this idea, but it has never been possible to prove beyond doubt that any such additions to the sporogenous tissue really take place; however, of the additions from segmentation of the outer of the two original cells (fig. 1) there cannot be any question after comparison of figs. 1–8.

It is interesting to compare these results with RUSSOW's drawings ('Vergl. Unters.,' Plate 9); his fig. 179 shows on the left side a sporangium of age intermediate between my figs. 1 and 2, and with virtually the same structure; while his fig. 177 corresponds substantially, though not in the minute details, with my fig. 3. Such correspondence, though not surprising seeing that the drawings refer to the same species (*E. arvense*), is certainly satisfactory.

After the sporogenous tissue has been thus laid down, the cells which lie above it divide by periclinal and anticlinal walls; some four or five layers of cells are thus formed (fig. 6), of which the outermost develops as the apical part of the wall of the sporangium, the rest of the wall being contributed by the superficial cells of the lateral parts of the sporangium; the cells directly surrounding the sporogenous mass assume the characters of a tapetum, while the intermediate cells become gradually compressed and finally disappear without any special modifications, as the period of maturity of the sporangium approaches. These later phases of the development having been more carefully followed in *E. limosum*, we may now proceed to examine the results of investigation of that species.

Equisetum limosum, L. (figs. 10–21).

It has been already shown that GOEBEL's account of the development in this species leaves some points uncertain; this is probably due in part to the very considerable variations of detail of the sporangia even in the same strobilus; how great those variations may be is shown by fig. 10, which represents three sporangia in juxtaposition with one another (*a*, *b*, *c*), together with the stalks of the sporangiophores which bore them (*sp.*); not only is there a great difference in size and outline of these sporangia, but also in the number of the sporogenous cells as seen in the transverse section, and even in the number of layers of cells composing the wall. Such variations of detail naturally increase the difficulties of tracing the course of development.

The earliest stages of growth have not been seen in *E. limosum;* but this is immaterial after the observations on *E. arvense*, and in face of GOEBEL's drawing ('Bot. Zeit.,' 1881, Pl. 6, fig. 1); for there is no reason to doubt the correctness of the cell-net there shown, in what is obviously a median section. The only question is the correctness of recognition of the archesporium: it will be seen from a study of older sections that the second cell, immediately overlying the shaded archesporial cell of GOEBEL's figure, should also be reckoned a part of the archesporium; as in

E. arvense, this cell is added to the first archesporial cell, and originates by a subsequent periclinal segmentation of the superficial cell.

The sporangia of *E. limosum* are usually less bulky than those of *E. arvense:* their apex is commonly more pointed, and the archesporial series may remain for a considerable time undivided by longitudinal walls: this is suggested by GOEBEL'S figure ('Bot. Zeit.,' 1880, Pl. 8, fig. 3), and is conspicuously the case with fig. 11, in which the archesporium consists of only a single row of three cells; such an appearance would be presented by the sporangium (*a*) fig. 10, if cut through radially. Other sporangia show the archesporium as a double row (as in fig. 12); it is to be noted here that the apical limits of the two rows do not exactly coincide, the row next the sporangiophore being longer than that more remote from it. Lastly, the sporangium shown in fig. 13 resembles more nearly the type of *E. arvense,* as regards the regularity of segmentation of the apical part of its sporogenous tissue, though the basal is irregular; it also has a rounded apex; the cells marked (?), adjoining the sporogenous tissue laterally, are of large size, and have dense protoplasm; it is possible that they may be lateral additions to the sporogenous tissue, but such additions have not been definitely proved to take place. Of older sporangia cut radially, two extreme examples have been drawn; of these, fig. 14 is of the more pointed type, and comes from near the apex of the strobilus; it will be noted that the limits of the sporogenous tissue on either side of the median line are unequal, and that, as in fig. 12, the sporogenous tissue is more extensive on the side next the sporangiophore than on that which is more remote; the result is a very irregular disposition of the tissues towards the apex. The other example (fig. 15) shows a very bulky sporangium with broad rounded apex: this comes from the lowest tier of sporangiophores, and directly adjoins the annulus. The segmentation has here been very regular, and conforms more nearly to that of *E. arvense* than does that of the large majority of the sporangia of *E. limosum.*

Of the tangential sections those shown in figs. 16, 17, 18 were from the same strobilus as the radial sections, figs. 11, 12, 13. Fig. 16 represents one of the simpler types of sporangium, in which the sporogenous tissue consists in part of only a single row of cells. Figs. 17 and 18 are of a more bulky type, especially the latter, while, in addition to the sporogenous tissue which is shaded, the cells marked (?) are of considerable size and contain dense protoplasm; it is here again a matter of doubt whether cells of other genetic rows are not added laterally to the sporogenous tissue derived from the median row. Fig. 19 represents a rather older sporangium of the more bulky type, from the same strobilus as those drawn in transverse section in fig. 10, and in longitudinal section in figs. 14 and 15; it shows a sporogenous tissue of even a more massive character than that of *b* (fig. 10), and corresponds probably most nearly in complexity of structure to the sporangium drawn in fig. 15.

The whole of these drawings serve to illustrate the considerable fluctuations of bulk and complexity of structure in the sporangia of this species, and this is quite in accord with the experience of GOEBEL ('Bot. Zeit.,' 1880, p. 551). The observations here detailed agree with his so far as regards the reference of the sporogenous tissue to a single axile row of cells, with reservations of some questionable cases where parts of lateral rows may contribute a few cells; but this has been actually demonstrated in no single case. I cannot, however, agree with him in referring the whole sporogenous tissue to a single cell of that row; here, as in *E. arvense,* additions are made to the primary archesporium by development of more superficial cells (marked × in figs. 12, 13, and 16, where they are clearly distinguished). The cells of the axile row sooner or later divide by longitudinal walls, and again subdivide in various directions so as to produce a sporogenous tissue, which, in longitudinal section, would appear to average about 72 cells.

Turning now to the cells which surround the sporogenous tissue, their arrangement is rather irregular, and the band of superficial tissue is usually thicker at the apical and lateral parts than on the anterior and posterior faces (figs. 10, 14); the sporogenous tissue is covered at the apex by three to five layers of cells, which are narrow, and are arranged with some approach to regularity. Of the tissues composing this peripheral band, the innermost row of cells develop as the tapetum, dividing by repeated anticlinal walls, and may thus be distinguished from the rest (fig. 20); the outermost series become enlarged and their walls strengthened, forming the permanent wall of the sporangium, while the cells which intervene are compressed, and their nutritive substances withdrawn as the sporangium approaches maturity.

As in other cases, the cells of the sporogenous tissue separate, round themselves off, and divide into tetrads. This process has been repeatedly the subject of detailed observation, and I do not propose to follow it further; there is, however, a fact of some importance which does not appear to have been noted by other observers, that is, the partial sterilization of the sporogenous tissue. It has been remarked above that an average number of sporogenous cells in a longitudinal section, before they separate and round themselves off, is 72, but the average number of these cells, as seen in one section after they are rounded off, is only about 44: the explanation of this reduction is to be found in the fact that a considerable number of cells become disorganized during the process, as is shown in fig. 21. Here it is seen that the tapetum is still a continuous band outside the sporogenous cells, though the cell-walls of the tapetum are disorganized, and the nuclei float freely in the continuous protoplasm. The outer sporogenous cells still form an external barrier, but certain cells of the sporogenous mass have lost their definite outline, their protoplasm has become irregular, and their nuclei have lost size and brilliancy, and differ materially from those of the rounded sporogenous cells: the number of cells thus altered in the small part drawn is 13, as against 30 which are rounded off. These numbers, rough though they are, will suffice to explain the discrepancy above noted. In fact, about one-third to one-quarter of the sporogenous cells are disorganized and do not form spores: their function is that of a diffused tapetum, and there can be no doubt that their substance contributes to the nutrition of the survivors. Ultimately the external tapetum makes its way between the rounded sporogenous cells, and then it is no longer possible to distinguish the nuclei and plasma of the external tapetum from those of the disorganized sporogenous cells. It will subsequently be shown that a similar breaking down of sporogenous cells takes place in other types of Vascular Cryptogams, and it must be recognized as one of the forms which *sterilization* of this tissue may be found to assume.

Results from Study of Equisetum.

1. The sporangium is Eusporangiate.

2. The essential parts of the sporangium, that is, the contents, are ultimately referable in origin to a single superficial cell.

3. The first division of this cell is periclinal : *the inner cell forms only part of the sporogenous tissue, to which addition is made of other cells derived by further segmentation of the outer cell.* The archesporium of *Equisetum* is thus shown to be not a single hypodermal cell in the sense laid down by GOEBEL

4. The tapetum is derived from the series of cells immediately surrounding the sporogenous mass.

5. *About one-third of the cells of the sporogenous mass are broken down and disorganized without forming spores ;* these serve physiologically as a diffused tapetum, and help to nourish the developing spores.

6. The superficial cells form the wall of the sporangium, while those between the tapetum and the wall are pressed out of shape and disorganized as development proceeds.

7. The sporangiophores and sporangia of *Equisetum arvense* when young are, on the average, of a more massive type and more regular segmentation than those of *E. palustre ;* and it is to be noted that the former is a terrestrial, the latter an aquatic species.

Theoretical Consideration of the Results.

Perhaps the most interesting point of detail in the results thus stated is that the archesporium of *Equisetum* is not, strictly speaking, of hypodermal origin, but that an addition is made to the first hypodermal archesporial cell by further segmentation of the superficial one. In this, it will be subsequently shown that *Equisetum* does not stand alone. In *Isoetes*, also, and in *Selaginella*, and, in rare cases, in *Lycopodium*, similar additions appear to be made to the sporogenous cells first laid down ; the cells thus added are shown in *Equisetum* to develop into spores, and are thus archesporial in their character. It will be seen that these facts will affect the generalization of GOEBEL, as given in the paper in which he introduced the idea of the archesporium ('Bot. Zeit.,' 1880, p. 569). He there states "that in all the Vascular Cryptogams which he investigated there is a hypodermal archesporium." GOEBEL assigns no lateral limit to the archesporial tissue as applicable for all cases, for, according to his description, the archesporium may be a single cell, a row of cells, or even a layer or sheet of cells (*loc. cit.*, p. 564). This my observations, to be detailed below, amply confirm. The only definite limit which GOEBEL assigns for all Vascular Cryptogams which he investigated is that of depth of origin; they are all hypodermal. In the strict sense, however, this is not the case in *Equisetum*. Accordingly, I do not see how any strict topographical definition can be applied to the archesporium which shall hold for all Vascular Cryptogams. It is true that in most Vascular Cryptogams, and probably in all, the archesporium is ultimately referable in its origin to the segmentation of one or more superficial cells. But what part of the shoot in these plants does not originate in this way? A statement of this fact would be in no way distinctive in plants in which one or more initial cells are commonly the ultimate parents of the tissues of all parts, whether deeply seated or superficial. *While the results of my observations on sporangia of Vascular Cryptogams will confirm* GOEBEL'S *statement that the sporogenous tissues are referable in origin to a definite cell or cells (archesporial cells), I find it impossible to give to these cells a strict topographical definition which shall apply in all cases.*

This conclusion need be in no way surprising, for it is plain, in the first place, that the segmentation which gives rise to the archesporium, in Vascular Cryptogams, is different from that in Phanerogams; in the latter the dermatogen is as a rule definite, and distinct in origin and segmentation from the subjacent hypodermal cells, which ultimately give rise to the sporogenous tissue.

In the second place the origin of the archesporium in the Musci is not uniform; for it has been shown by WALDNER ('Die Entw. d. Sporogone v. *Andræa* u. *Sphagnum.*' Leipzig, 1887), that while in *Sphagnum* the archesporium is formed from the endothecium, in *Andræa* it is derived from the amphithecium, the latter is also the case for other Mosses.

The case of the Anthoceroteæ has also been noted above (p. 489); in these plants there is absence of uniformity in origin of the sporogenous tissue, within the limits of the family. This I take to be a most instructive example in connection with the present question. While there is, thus, want of uniformity within the Bryophyta in the depth of origin of the archesporium, there is also a difference in its mode of origin as we pass from the Bryophyta to the Vascular Cryptogams, and again, in point of segmentation, as we pass from the latter to the Phanerogams. In view of these variations it need be no matter for surprise that in the Vascular Cryptogams themselves the mode of origin of the archesporium is not susceptible of a strict topographical definition which shall apply for all cases.

Equisetum being a strobiloid type, in accordance with our working hypothesis, we shall look upon the strobilus as the counterpart of a sporogonial head, while the apex of the strobilus will then correspond to the apex of a sporogonium (see p. 492).

As regards the segmentation of the apex I see no difficulty in the present case, for the apical cone of *Equisetum,* as seen in the strobilus, is in many respects similar to that of certain sporogonia of Bryophytes ; few would see in the difference between a two-sided and a three-sided cell, or between a three-sided pyramid and a growth with more than one initial, a serious objection to such a comparison as I suggest.

The sterile central part of the strobilus, with its vascular bundles, would be the counterpart of a columella. It is, doubtless, more bulky, and its structure more complex, but, as regards its topographical relation to the spore-production, it is undoubtedly similar to the columella of Bryophytes. Now, among the Anthoceroteæ, there is found great variation in the bulk of the columella ; in the genus *Notothylas,* especially, such variations are seen. I accordingly look upon the relatively greater bulk of the central sterile mass in *Equisetum* as no obstacle to its recognition as the counterpart of the columella.

The form of the very young strobilus is clearly like that of a sporogonial head ; the chief difference lies in the simplicity of external surface of the Bryophytic sporogonium and its connected archesporium, while, in *Equisetum,* the surface produces outgrowths (the sporangiophores), and the archesporia are isolated. But the appearance presented during development is very suggestive, and may with propriety be thought to give a clue to the origin of the more complex structure. The young strobilus has first a smooth surface, on which undulating swellings appear, as already noted by HOFMEISTER and by GOEBEL. At an early stage, the sporangia may be recognized as originating at certain points on these outgrowths (compare figs. 1–4, Pl. 42), certain superficial cells, by their segmentation, supplying the essential parts of the sporangia. On our hypothesis, we should see in these cells and the products of their segmentation, the isolated remains of a largely-sterilized potential archesporium, while the fact that they are carried out upon the massive sporangiophores need in no way disturb this comparison of the archesporial cells themselves. It may, however, be objected that, in *Equisetum, superficial* cells provide the essential parts of the sporangia ; but this again is no real difficulty, for, ultimately, the same is the case in many Bryophytes ; the amphithecium is, in the young state, a series of superficial cells, and it is this layer which in many cases yields the sporogenous tissue. But, in this connection, the absence of strict uniformity of origin of the archesporium in the Bryophyta is specially important. The gradual appearance of the columella, and relegation of spore-production to more superficial tissues is illustrated in the Anthoceroteæ ; if such a modification were carried but a little further, if the columella were more bulky, and the definite specialization of archesporia deferred, the result, *as regards locality,* would be such as is seen in *Equisetum.* There is, however, the essential difference of the archesporium being in the Bryophyta one continuous band, in *Equisetum* isolated patches ; at present, we have no direct evidence before us how such a change took place, but, referring again to the analogy of the Anthoceroteæ, the origin of the columella, by grouping of sterile cells, has been concluded by LEITGEB (see p. 489).

We see that, in *Anthoceros,* a large proportion of the cells resulting from the archesporium are developed as sterile cells; a grouping of these together might produce such a condition as is seen in *Equisetum,* viz., the isolation of those cells which still remain fertile (archesporia), while between them extensive tracts of sterile tissue would intervene. Such would be an extreme example of the septate condition, and it will remain to inquire whether any evidence is to be found among other Vascular Cryptogams as to the origin of sterile septa from a continuous potential archesporium. In the meanwhile, we may note with additional interest the presence of a large number of sterile cells in the young sporangia of *Equisetum,* and, though they do not develop as elaters with thick walls, still in their condition of sterility they may properly be compared with those of the Liverworts, especially of the type shown in *Oxymitra.*

Another question will be whether from other types of Vascular Cryptogams evidence can be gained of the origin of upgrowths (sporangiophores) which would raise the sporangia beyond the surface of the part on which they are produced; such evidence would be of peculiar value in its bearings upon the question under discussion.

In any discussion such as that before us, the facts concerning the strobili of certain fossil forms will have to be considered. Whatever opinions may be held as to the nearer or more remote kinship of modern *Equiseta* to the Calamarieæ, there can, I think, be little doubt that the strobilus of a modern *Equisetum* as a whole is the homologue of the whole spike-like fertile branch in the latter group. Assuming this to be granted, we see on comparing these several strobili that there is some variety in their construction, and in the relations of the component parts one to another. Such points will have to be considered in the general discussion of the question, which will be taken up later.

In the meanwhile I see in the case of *Equisetum* no *à priori* objection to our working hypothesis; the details of development would rather support it. But before it can be seriously entertained, some more consecutive evidence will be required that formation of sterile masses of tissue from a potential archesporium does occur; we shall also inquire whether it may be concluded, on comparative grounds, that septa have been produced within any naturally allied series of Vascular Cryptogams, thus dividing into separate parts an originally continuous archesporium.

LYCOPODINEÆ.

The Lycopodineæ are also strobiloid forms, to which our working hypothesis may be applied. In examining them, we may be prepared to see in the strobilus the counterpart of a sporogonial head, while certain of the vegetative parts may have resulted from further development of a sterile part corresponding to a seta. In the latter category may, perhaps, be placed the protocorm of TREUB, with the leaves (protophylls) which it bears; it will, however, be shown that the majority of the sterile leaves of certain Lycopods are more probably to be looked upon as sterilized sporophylls. These ideas will be applied in the study of various Lycopodinous forms which will now be taken up.

PHYLLOGLOSSUM DRUMMONDII, KUNZE (figs. 22–33 and fig. 92, *a*, *b*, *c*.).

The vegetative organs of *Phylloglossum* are now fairly well known, both as regards external form and internal structure. The earlier observations of METTENIUS[*] have been extended by M. BERTRAND,[†] who investigated chiefly the mature structure, and by myself as regards the germination of the tuber, and the formation of the new vegetative parts from it.[‡] These two researches, conducted separately and published almost simultaneously, led to virtually the same conclusion, viz., that we may regard *Phylloglossum* as a form which retains, and repeats in its sporophyte generation, the more prominent characteristics of the embryo as seen in *Lycopodium cernuum.* This conclusion was based on comparison of *Phylloglossum* with young stages of development of *Lycopodium cernuum,* as described by Dr. TREUB in his earlier memoir on that plant;[§] but the similarity in certain points is now seen to be even more striking since the publication of this author's more recent observations on the embryology of this plant;[||] while assenting to the general conclusion, Dr. TREUB prefers to give the thesis a slightly different form, by inverting it, and asserting rather that in their young state *Lycopodium cernuum, inundatum,* and *salakense* repeat the *Phylloglossum.* In view of Dr. TREUB's theory of the *Protocorm,* this amendment may be accepted. He states the theory as follows :—[¶]

"The embryonic tubercle in the Lycopods is *a rudimentary organ.*" "The organ theoretically admitted as occurring in the ancestors of actual Vascular Cryptogams, and styled above 'The predecessor of the leafy shoot as it is now seen in the genus *Lycopodium,*' exists even at the present day as a transitory stage in the genus *Lycopodium.* This *organ is none other than the embryonic tubercle.*" Further, "I propose to give the embryonic tubercle of the Lycopodiums the name of the *Protocorm.*" Later, referring to *Phylloglossum,* Dr. TREUB says: "it will be superfluous to say that, to me, the tubercles of *Phylloglossum Drummondii* are to be looked upon as protocorms, playing still a real and considerable part. The protocorm of multiplication of *Phylloglossum* has become a much more specialized organ than in the Lycopodiums."

From the above quotations, which put the whole matter on a firmer footing than before, it appears that Dr. TREUB would endorse the last words of my former memoir on *Phylloglossum*, viz., that "it is a permanently embryonic form of Lycopod"; in fact, as he states,* *Phylloglossum* "would represent a more ancient group than that represented by living Lycopodiums."

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[*] 'Bot. Zeit.,' 1867.

[†] 'Arch. Bot. du Nord de la France,' 1885, p. 70.

[‡] 'Phil. Trans.,' 1885.

[§] "Études sur les Lycopodiacées," 'Ann. du Jard. Bot. de Buitenzorg,' 4, p. 107.

[||] 'Ann. du Jard. Bot. de Buitenzorg,' 8, p. 1.

[¶] *Loc. cit.*, 8, p. 30.

This view, however, is not universally admitted. M. BERTRAND, while recognizing the similarity between the early stages of *Lycopodium cernuum* and the adult *Phylloglossum*, remarks "It is singular, in the present case, that *Phylloglossum* is superior to the Lycopods, and still that its adult state is but a reproduction of an embryonic stage of the latter. Here is a case of retrogression, which has as its prime cause the semi-aquatic habit." I confess, with all respect to M. BERTRAND, that the anatomical characters on which he chiefly relies for assigning relative positions to the Lycopods do not seem to me a sufficient reason for placing *Phylloglossum* higher in the scale than *Lycopodium*. As to the semi-aquatic habit, it seems to me that it is precisely in such positions that the most interesting early forms of the sporophyte might on *a priori* grounds be expected to occur; if, as I have suggested elsewhere, antithetic alteration be an adaptive development closely connected with the progression from water to the land, then the semiaquatic flora should include some of the earliest types of development of the sporophyte.† Accordingly, I am disposed to look upon *Phylloglossum as relatively a primitive form*, and for this reason I shall give it the first place in the description which is to follow.

One of the most marked characteristics of *Phylloglossum*, and one by which it is distinguished from species of *Lycopodium*, is that the transition from the leaves borne by the protocorm to the sporophylls of the strobilus is usually a sudden one. The zone of intercalary growth, by the extension of which the strobilus is carried up, appears to be a natural limit between the vegetative leaves on the one hand, and the sporophylls on the other. In one specimen, represented in fig. 22, a single sporophyll is seated at some distance below the rest of the strobilus; it has, however, a sporangium in its axil, and is therefore to be looked upon as a sporophyll which was left behind in the course of intercalary growth; but it is also of larger size and more succulent development than normal sporophylls, and may therefore be actually an intermediate step between the sporophyll and those leaves (protophylls) which are borne by the protocorm. On the other hand, it is not unfrequently found that the last of the protophylls is smaller than the rest; this was shown in figs. 18, 20, 25, and 27, of my former paper, and alluded to in the text on pp. 670, 671, and 675.‡ The position of these leaves is close to the base of the strobilus in those plants which bear sporangia; these leaves, again, are probably transitional steps between the typical protophyll and the sporophyll; they are, however, inconstant, both in form and occurrence, and commonly the transition is a sudden one. I think it probable that the part described by M. BERTRAND under the name of the "organ of METTENIUS,"* is simply one or two rudimentary leaves of this nature. This was suggested by M. BERTRAND himself (*loc. cit.*, p. 197), but whereas he describes this organ as of constant occurrence, there was very little constancy in its appearance in the specimens which I have examined.

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* *Loc. cit.*, p. 73.

† 'Annals of Botany,' vol. 4, p. 347, &c.

‡ 'Phil. Trans.,' 1885.

The strobilus itself is almost always simple, but one specimen, grown in the Glasgow Botanic Garden, shows a branching (fig. 23) into two unequal limbs. The plant was a weakly one, and neither of the strobili appeared well developed; it may therefore be looked upon as an abnormality, though it is interesting for comparison with the branched strobili of various species of *Lycopodium*.

For comparison, on the one hand with the structure of the mature protophylls as described by M. BERTRAND† and by myself,‡ and on the other with the protophylls of *Lycopodium cernuum*, as described by M. TREUB,§ I have made drawings of young states of *Phylloglossum*. Fig. 24 shows a whole plant, such as that of fig. 8 of my former paper, in median longitudinal section, while fig. 25, i., ii., iii., are successive transverse sections of a single leaf. It is true that no distinctive characters are apparent from these sections, but the rarity and morphological importance of this plant justify the representation of such details, even though the bearing of them may not be obvious at the present moment.

Applying our working hypothesis to *Phylloglossum*, which on grounds above stated we recognize as a relatively primitive type, we should see in the protocorm the counterpart of the seta of Bryophytes. It is enlarged it is true, and bears appendicular organs (protophylls and roots), but these are distinctly primitive in their form; the leaves are arranged in a rather irregular fashion, the roots are exogenous and the whole character of this part of the plant is such as to fall in with the hypothesis. The distinction between this vegetative region and the strobilus is unusually definite, more so than in other Lycopods, while there is an entire absence of that intermediate vegetative region which forms the greater part of the plant of *Lycopodium*, even in such species as still show the characters of a protocorm in their embryonic stages. In the strobilus we should see the counterpart of the sporogonial head; as in the case of *Equisetum*, it is more complex in external form than the sporogonial head, bearing appendicular organs, and separate sporangia; but the same arguments as have been used in the case of *Equisetum* will apply also here in meeting antecedent objections on these grounds to the comparison which I suggest. The detailed examination of the strobilus will now be proceeded with.

The strobilus has been described in minute detail by M. BERTRAND,‖ as regards

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* 'Arch. Bot. du Nord de la France,' *loc. cit.*, p. 74.

† *Loc. cit.*, p. 174.

‡ 'Phil. Trans.,' 1885, p. 673, and figs. 36, 37.

§ 'Ann. d. Jard. Bot. d. Buitenzorg,' 8.

‖ *Loc. cit.*, pp. 120–131.

its mature structure, but developmental data are at present wanting. This lacuna I am able partially to fill, from observations on specimens reared from tubers in the Glasgow Garden. The youngest state of the sporangium seen in radial section is that shown in fig. 26. The section includes the apex of the strobilus, which is occupied by a conical initial cell; round this are segments disposed with some regularity, but it is difficult to refer the whole growing point in origin to this single initial. A single initial was not found either at the apex of the mature tuber, nor of the young one, and sufficient material was not at hand to decide the time of its appearance at the apex of the strobilus, or whether it be constant in occurrence, or in form. Below the extreme apex the youngest leaf (1, ii.) appears as a broadly convex outgrowth, without any single initial, while the next older sporophyll (s^1) is already far advanced, and bears in its axil the young sporangium. This is a multicellular outgrowth, of which the cells, as seen in this section, are referable in origin to a single parent. Segmentation has, however, gone so far that a single archesporial cell (a) is completely surrounded by others, and occupies a rather deeply-seated position. Fig. 27 shows another section through the same sporangium (which, as in *Lycopodium*, is a sausage-shaped outgrowth, and may thus be traversed by numerous planes of radial section). Here the segmentation is more regular, and the archesporium appears divided into four cells by very delicate walls, which the treatment of the previous section had probably made invisible. The cells below the archesporium are also showing the first signs of that activity of growth and division, which results in the formation of the stalk of the sporangium. Fig. 28 shows a rather later state with less regular segmentation, while in fig. 29, the first periclinal divisions are appearing in the cells of the wall of the sporangium. (N.B. This section is not exactly median.) Finally in fig. 30 is seen a sporangium in which all the essential parts are present. The enlarged head is borne upon a short and rather massive stalk, and it is bounded externally by a wall composed for the most part of two layers. Of these the inner would divide subsequently, and the inmost layer thus formed would be the tapetum. The basal part of the tapetum is already present as the irregular series of cells which adjoin the base of the sporogenous mass, the latter is already showing signs of the separation and rounding off of its cells preparatory to the formation of the tetrads. Taking all these facts together it is plain that the development of the sporangium of *Phylloglossum* corresponds in essential points with that of *Lycopodium Selago*, as laid down by GOEBEL,* or as described more in detail in later pages of this memoir (p. 511, &c.).

To gain an adequate knowledge of a solid body such as the sporangium of *Phylloglossum*, transverse and tangential sections must also be examined; but, owing to the small quantity of material, the details could not be so completely worked out as they will be in some species of *Lycopodium* to be dealt with later. Transverse sections through a sporangium of age corresponding to fig. 28, show that the archesporial cells form a series of which the number is at least four, and is probably larger (fig. 31); the section shows the sporangium united both with the stem and the sporophyll, the plane of section must therefore have been about the dotted line in fig. 28, and the two will mutually explain one another. Fig. 32 again shows part of an older sporangium in similar section, where the wall has already divided into two layers, while the sporogenous cells still form a continuous tissue, and have not yet completed the divisions before the separation of the spore-mother-cells.

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* 'Bot. Zeit.,' 1880, p. 561.

Finally a tangential section (fig. 33) of a sporangium rather younger than that of fig. 32 shows the form of the sporogenous mass, which is curved in a sinuous fashion, while the cells are obviously arranged in groups which show their mode of origin from pre-existent parent-cells; but each of these groups does not represent the whole product of one archesporial cell; probably each of the latter gives rise to two or even three of the groups there clearly defined. I am not able to state definitely the number of archesporial cells in this plant, but it is probably about six. Below the sporogenous tissue is the formative tissue of tapetum and stalk, of which the cells have obviously undergone repeated divisions, so as to raise the sporogenous mass up from its originally deep-seated position; the point marked (×) is the middle of the sausage-shaped sporangium, only half of which could be shown in the figure.

The general form of the sporangium as it approaches maturity, and its relation to the sporophyll and axis, will be seen from figs. 92 (*a*, *b*, *c*), and it is to be noted how closely the sporangium is surrounded by the sporophylls, and laterally by out-growing flanges of the axis, so that it is almost completely protected from evaporation from its surface, or from the direct sunlight, during its earlier period. The form of the sporangium is slightly curved (fig. *b*), and it is inserted by a short and moderately massive stalk close to the axil of the sporophyll.

Taking all the characters together, the strobilus of *Phylloglossum* is, both in its development and in its mature structure, strikingly similar to a simple strobilus of some species of *Lycopodium;* comparing the sporophyte of these plants as a whole, the most salient points of difference are first the size, and secondly *the absence from Phylloglossum of any representative of the leafy and often branched vegetative axis,* which as a development of considerable, often of great extent, precedes the production of strobili in *Lycopodium.*

Summary for Phylloglossum.

The most important results from this examination of *Phylloglossum* for purposes of our present comparison are these :—

1. The abrupt transition (with only few and inconstant intermediate steps) from the protocorm with its protophylls, to the strobilus with its sporophylls and sporangia.

2. The close similarity of the strobilus to that of *Lycopodium.*

3. The origin of the sporangium corresponds in detail to that of some species of *Lycopodium,* such as *L. Selago.*

4. The archesporium consists of about six cells, only one of which appears in each radial section.

LYCOPODIUM.

In the observations above described, and in those embodied in other works referred to, I see no material obstacle to the application of our working hypothesis to *Phylloglossum,* according to which the protocorm would be compared with the sterile seta of Bryophyta, of which it would be an elaborated example; the strobilus would also be an elaborated type of sporogonial head. It must, however, be remembered that the embryology of *Phylloglossum* is still unknown, while the sexual generation has never been seen; till observations on these are made, such a question cannot be considered as finally settled.

The relations of parts are by no means so obvious in the genus *Lycopodium;* in certain species, as already shown by TREUB, the protocorm is represented in embryonic stages (*L. inundatum, salakense, cernuum*), but in these it plays an unimportant part, as compared with the vegetative development which follows, and the question will arise how this more prominent vegetative phase of *Lycopodium* is to be regarded. The strobilus in many species is a clearly differentiated part of the plant (*e.g., L. clavatum*); in other species, however, there are peculiarly alternating sterile and fertile zones on the plant (*e.g., L. Selago*), and the question for us will be how are such characters to be harmonized with what has been seen in *Phylloglossum,* and how will they fall in with our working hypothesis? But before such questions can be discussed, the detailed description of observations which have been made on *Lycopodium* must be given.

The most detailed descriptions hitherto published of the development of the sporangium of *Lycopodium* are those given for *L. Selago* by GOEBEL,* and by SADEBECK† for *L. clavatum.* These descriptions are based chiefly upon radial sections through the strobilus, and though the appearance in tangential section is alluded to, no detailed description is given of the tissue so exposed; transverse sections appear not to have been examined by either writer. Obviously sections will be required in all three directions, radial, tangential, and transverse, in order to obtain a clear understanding of the structure and development of the sporangium; this is more especially needed where, as in this genus, the sporangium is large and complex in structure. SADEBECK remarks‡ that the recognition of the details of the archesporium is a matter of no great moment; in dealing with plants, which are allowed to be the surviving relics of a flora with a great history in the past, and to show affinities to the Bryophyta, all details have their importance, more especially those which relate to the primary spore-producing members. GOEBEL appears to have examined only one species in detail, and to have assumed that the details are virtually the same for all; in so comprehensive a genus as *Lycopodium* it is desirable to examine and compare a number of species, of as divergent types as possible.

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* 'Bot. Zeit.,' 1880, p. 561, &c.

† SCHENK's 'Handbuch,' vol. 1, p. 313

‡ *Loc. cit.,* footnote, p. 318.

Accordingly a very large number of serial sections have been prepared from different species of the genus; the strobili have been cut radially, tangentially, and transversely, and upon these sections a comparative study of the development of the sporangia from their earliest stages has been based. The results will now be described in detail, and it will be shown that there is not only a considerable variety in the form of the sporangium in different species, but also in the mode of origin and number of the archesporial cells.

It may further be added that the sections were cut in series, by the rocking microtome: being extremely thin, there was no need of clearing by potash or other agents: as each section included only one layer of cells, or at most parts of two, there was no need of focussing down into the thickness of the section in order to obtain results, a method which has frequently been a source of error in developmental studies. Finally, the recognition of the archesporium in early phases of development has not been based merely upon the refractive power, or granular character of the cell-contents, but in cases of doubt the decision has been arrived at by comparison of other sections illustrating the course of development, rather than by recognition of differential characters in the individual specimen; for these differential characters often appear relatively late, and are, at best, an uncertain guide.

L. Selago. L. (figs. 34–49, and fig. 92, *d*, *e*, *f*.).

This species having been the subject of the most detailed previous study, will be first described. The sporangium originates on the upper surface of the sporophyll, and close to its base; it is, at the time of separation of the tetrads, a slightly curved body, of which the form as seen in radial, tangential, and transverse sections will be best recognized by reference to the figs. 92, *d*, *e*, *f*. It is specially to be noted that in the radial section the stalk is narrow in proportion to the size of the head of the sporangium, while, as seen in tangential section, the stalk measures rather less than one-third of the total width of the sporangium. The sporophyll covers in the young sporangium only partially; and, together with the next higher leaf and flanges of the stem below the insertion of the lateral leaves, forms a much less complete protection than is the case in some other species.

In examining radial sections through the sporangium those have always been selected which include the vascular bundle of the sporophyll; it is not sufficient in the case of a sporangium of tranversely elongated form, like that of *Lycopodium*, to ascertain that the section of the strobilus is strictly radial, for in such a section the sporangium may be traversed obliquely; if, however, the sporophyll be cut radially, so also must be the sporangium which it subtends. As seen thus in radial section the sporangium appears to originate from a single cell, but this is only one of a series which lie at the base of the sporophyll. This cell divides by anticlinal walls, so disposed as to cut off lateral parts from a larger cell which lies between them (× figs 34, 35); the lateral cells undergo subsequent subdivision, but apparently not according to a strict rule, as will be seen on comparison of figs. 35 to 41; the larger central cell (×) has a square base; by periclinal walls there are cut from it a basal cell (iii) which after further subdivision contributes to the central part of the stalk; and a superficial cell (i), which forms part of the wall of the sporangium: the cell (ii), which lies between these, is the *archesporium*, and it is thus unicellular, as seen in radial section. The description thus far coincides with that given by GOEBEL, and fig. 36 may be compared with his fig. 8; excepting some differences of position of the less important walls the drawings correspond; it is not however to be expected that the correspondence should extend to minute details, in the case of relatively bulky masses of tissue such as these. I am unable to endorse the details of the subsequent steps as described by GOEBEL. He illustrates by his fig. 9 how, at a later stage, the sporangium consists of a wall of a single layer of cells, and three rows of cells enclosed by it. The archesporium is stated by him to be derived from the central more strongly-growing row, while lateral rows are curved to one side, and take no direct part in the formation of spores; it is to be noted that GOEBEL gives no account of how these three rows of cells originate, and in accurately radial sections I have never seen such an arrangement. The structure of the sporangium, which I found to be typical though not constant at this later stage, is that shown in fig. 37; the cell (i) of fig. 36 has undergone anticlinal divisions, so that the wall, of which it forms a part, consists of a single line of cells; cell (ii), which is the archesporium, divides longitudinally and transversely, so as to form a group of sporogenous cells, which abut on three sides directly upon the wall of the sporangium, while the base is in contact with the tissue derived from cell (iii); this has undergone longitudinal division into two, and these cells divide repeatedly in a transverse direction, so that two primitive rows of cells, not three, occupy the interior of the stalk. But this almost diagrammatic regularity may be often absent, and some sporangia present appearances such as those in figs. 38 and 39; the explanation of such irregularities as these is to be found in the fact that the archesporium consists not of one cell, but of a row of cells, and that the walls separating these do not always run in radial planes, but sometimes obliquely, so that even a perfectly radial section, cut very thin, may include parts derived from distinct archesporial cells; this has probably been the case for the parts *a* and *b* of the figs. 38 and 39. In the latter the periclinal division of the cells of the wall has begun; this takes place as GOEBEL has described it, the superficial cells dividing periclinally; the inner of the resulting layers again divides, the innermost layer being the tapetum; there is often some irregularity in the details, and it is to be specially noted that the second divisions are delayed at the apex, where the line of dehiscence of the sporangium will be (*d*, fig. 40). The head of the sporangium meanwhile enlarges, the sporogenous mass of cells having grown, and having undergone repeated divisions the spore-mother-cells round themselves off, separate from one another, and are freely suspended in a fluid mass; they then divide into tetrads in the manner already well known. The structure of the radial section of the sporangium at the time when all the essential parts are laid down, is thus shown in fig. 41; the wall consists typically of three layers, of which the outermost is the permanent wall; irregularities occur, however, by which the number of layers is in part increased to four, or even more layers; the stalk, originally consisting of three rows of cells, remains permanently narrow as compared with other species, and shows 5–7 rows of cells.

Since the sporangium, when mature, is a reniform body, tangential sections, which follow the plane of curvature, will give more certain results than transverse sections in determining the origin, number, and form of the archesporial cells. Hitherto, little is definitely known on this point. GOEBEL does not give any detailed account of the tangential section (*loc. cit.*, p. 564). Fig. 42 shows a tangential section, through a sporangium of nearly the same age as fig. 36, and the corresponding cells are similarly numbered. It thus appears that the number of archesporial cells (which are here shaded) is at least seven, but a comparison of other sporangia shows that the number may vary. Examination of their arrangement, and relations to one another, shows that they are not referable in origin to a single cell, though this was suggested by GOEBEL as not improbable. It seems rather that in this section they are referable to at least three, but a comparison of other sporangia has not disclosed any fixed number of archesporial cells, nor any definite mode of their origin. The sporangium, which appears at first (fig. 42) as a simple projection, soon begins to extend right and left (fig. 43), projecting beyond the limits of its stalk, and assuming ultimately the kidney-like form shown in fig. 92, *e*; the archesporial cells meanwhile divide (figs. 43 and 44), in a manner which explains itself from the figures; the cells of the wall also divide periclinally, and in accordance with what has been seen in radial sections. The tissue derived from the cells marked (iii.), and the adjoining cells, is worthy of attention: the cells grow and divide repeatedly, forming a massive pad below the sporogenous tissue, which apparently presses the latter outwards, especially at the central part, and the whole sporangium assumes the curved form. This pad of neutral tissue is smaller here than in several other species, but it is well to note its existence, and as it will be an important feature in the subsequent argument, it may be called the *sub-archesporial pad.*

It remains to describe the appearance of the sporangium in transverse section. This has been alluded to by GOEBEL (*loc. cit.*, p. 564), and the multicellular character of the archesporium was observed by him, but no drawings were published. The sporangium appears as an elongated and massive projection, and when viewed externally and from above, shows no clearly-defined series of cells which could be distinguished as the cells (ii.) of figs. 36 or 42 ; the segmentations seem to be irregular, and this will coincide with the difference of details of segmentation as seen in other sections (fig. 45). The series of archesporial cells being curved, it is clear that a transverse section will cut only the middle cells of the series transversely, while those right and left from them will be cut obliquely ; this must be remembered in the interpretation of the sections. When cut transversely (fig. 46), the young sporangium shows the series of archesporial cells, of which six or more may be traversed. The wall of the sporangium consists at this stage of a single series of cells ; at the poles of the sporangium the appearance of a doubling of the walls may be presented, but if reference be made to fig. 42, and the plane of section be taken as the line *s*, *s*, it will then be understood how this apparent doubling comes about. The sporangium, in such sections as fig. 46, is adherent to the sporophyll. This is explained by reference to fig. 36, in which the line *s*, *s* will indicate the plane in which the sporangium of fig. 46 has been cut. The subsequent development is illustrated by figs. 47, 48, and 49, and, after the foregoing descriptions, these will call for no detailed explanation. It may be noted, however, that the wall of the sporangium on the side next the sporophyll is commonly thicker than on the adaxial side ; this may be seen early in the radial sections (figs. 37–39), and comes out clearly in the transverse sections also (figs. 48 and 49).

The origin of the tapetum is, as GOEBEL has described it, partly from the cells which form the wall of the sporangium, but partly also from the products of cells (iii.) in figs. 36 and 42. The question may be brought up whether the whole of the sporogenous mass be really derived from the cells recognized as the archesporium, or whether other cells may also contribute to the mass ; for instance, such cells as those marked (×) in figs. 46 and 47 might suggest the idea of such additions ; other sections, somewhat irregularly cut, might also be thought to support this ; it has, however, been shown that the cells marked (×) owe their appearance to the oblique direction in which the plane of section traverses the lateral parts of the sporangium, and a similar consideration of the details in other cases suffices to show that in this species the sporogenous mass is referable in its origin entirely to the archesporium as above described.

It is well known how *L. Selago* bears on one and the same axis successive fertile and sterile zones ; the character of the leaves, however, varies but little, the sterile foliage leaves being in all essential points similar to the sporophylls. An examination of the leaves about the limits of these zones shows that in the axils of those apparently sterile, a more or less completely arrested sporangium is commonly to be found, so that the transition from the one to the other is a gradual one. The simple fact, so easily observed in this species, is found also to hold for others, and its importance will be brought out more prominently on a later page (p. 535).

Results from study of L. Selago. L.

The chief facts regarding the development of the sporangium in *L. Selago* may be summarised as follows :—

1. The sporangium originates at the base of the sporophyll, as a transversely extended cushion, consisting of many cells, arranged without strict regularity.

2. The archesporium consists of one row of hypodermal cells, six or more in number, which give rise to the whole of the sporogenous mass.

3. The tapetum is derived partly from the primitive wall of the sporangium (from the innermost of the three layers resulting from its division), partly from the cells which lie directly below the archesporium.

4. The pad of tissue below the archesporium grows into a convex mass, which projects so as to give a curved form to the sporogenous tissue; this is however less marked than in some other species.

5. The stalk of the sporangium is narrow, consisting at first of three rows of cells as seen in radial section ; these subsequently increase by division to five, six, or seven.

6. The plant shows successive sterile and fertile zones, and there is no sharp limit between the fertile strobilus, and the sterile, or vegetative part ; about their limits arrested sporangia are to be found in the axils of the leaves.

L. phlegmaria. L.

Certain other species of *Lycopodium* which have been examined show a near approach to *L. Selago* in the characters, both mature and developmental, of the sporangium ; of those we may take, first *L. phlegmaria,* and it is somewhat remarkable that the similarity should exist in species which in habit and habitat are so different as these two species are. The general form of the sporangium and its relation to other parts of the strobilus are shown in figs. 92, *g, h, i* ; it will be noted that the similarity to *L. Selago* is most pronounced in the radial sections (figs. 92, *d, g*) ; in the tangential section the sporangium of *L. phlegmaria* is much more curved, and the stalk much narrower than in *L. Selago* (figs. 92, *e, h*) ; this character is well seen from the earliest stages of development (fig. 50), which also shows that the archesporium is referable in this species to not more than four, and probably even to two cells, while the stalk is also referable to the division of two cell-rows.

L. nummularifolium. Blume.

There is an obvious similarity between the strobili of this species and of *L. phlegmaria.* Examination of sections of the sporangia shows close similarity of details, so that there is no call for a special description; it may, however, be remarked, that occasionally extra periclinal divisions take place in the wall of the sporangium, thus increasing the mass of tissue composing it. Such divisions are occasionally seen in *L. Selago*, but are a characteristic feature in *L. dichotomum* (see below).

L. carinatum. Desv.

A form of the sporangium similar to that just described is found in *L. carinatum*, though in this species the actual size of the sporangium is much greater than in either of the preceding species. An examination of figs. 92, *n, o, p*, will show the resemblance to *L. phlegmaria*, both in the form of the sporangium, and the proportionally delicate stalk, and also in the lax manner in which the young sporangium is protected externally by the axis and sporophylls; all these peculiarities are thus shared by the four species which accordingly form a natural group as regards this character. In fig. 51 is shown a transverse section of the sporangium of *L. carinatum*, cut so as to traverse the sub-archesporial pad (*s.p.*) at a point immediately above the insertion of the stalk; this was drawn for purposes of comparison, and will be referred to later on. The shaded portions represent the sporogenous tissue. Specimens of this, and of the two preceding species, were kindly sent to me from Buitenzorg, by Dr. Treub.

Lycopodium dichotomum. Jacq. (= *L. mandioccanum.* Raddi.)

Specimens of this species were supplied to me from the Botanic Garden of Brussels. These show the sporangium to be similar as regards form to those of *L. phlegmaria* and *carinatum* (fig. 92) though the stalk is somewhat more massive, and the sub-archesporial pad is more largely developed. The chief interest, however, in the sporangia of this species lies in the fact that the wall of the sporangium is of unusual thickness. A detailed examination shows that the wall of the sporangium consists of some 4–7 layers of cells (figs. 52, 53); the number is not exactly defined, nor is the arrangement of the cells very regular; the outermost layer develops with thicker walls, as in other species; the innermost is the tapetum, while between these intervene several layers of thin-walled cells, which evidently have been increased in number by periclinal divisions (fig. 52). The development shows that this is the case, and that the difference between this and other species is due to additional periclinal divisions in the wall, and not to the contribution of tissues from the sporogenous mass to the tissues of the wall.

The interest of this departure from the usual type of *Lycopodium* rests on comparison with other forms; it will be shown later, that in "Brown's Cone" of *Lepidostrobus* the wall of the sporangium is more bulky and complex in structure than in other *Lepidostrobi*, or in most species of *Lycopodium;* it is generally known, also, that the wall of the sporangium of *Ophioglossum* is rather similar in structure to this of *L. dichotomum;* at present it will suffice to note these facts, which will be dwelt upon more fully at a later page. But even in sporangia of *L. Selago* and

L. nummularifolium a tendency towards this more bulky development of the wall is to be seen, especially near the base of the sporogenous mass; a comparison of figs. 40, 41, 49 of *L. Selago* shows that periclinal divisions have here and there increased the thickness of the wall to four layers in the lower part of the sporangium; we have but to imagine such divisions to extend upwards and to be more numerous, and the more complex wall of the sporangium as in *L. dichotomum* would be the result.

In other respects the development and structure of the sporangia of this species do not present characters requiring special description.

L. inundatum. L.

We may pass on now to species in which the sporangium is, even from the initial steps, of a more bulky character than in the *Selago* type. *L. inundatum* may be taken as an intermediate example (figs. 92, *k*, *l*, *m*); here the stalk is shorter and more massive than that in the preceding species, while the form of the sporangium approaches more nearly to that of *Phylloglossum.* The details of protection of the sporangium while young by the other parts of the strobilus also resemble those of *Phylloglossum,* though the protection is even more complete than in that plant.

Turning to the early stages of development it is seen that the sporangium originates as a more massive structure, showing a gentler and wider curve as it arises from the sporophyll. The sporogenous tissue appears here to be derived not from a single archesporial cell as seen in radial section, but two at least take part in its formation (fig. 54, shaded cells), while their relations are such as to show that the periclinal divisions, by which they were separated from the superficial cells, were formed independently in the two adjoining cells. Traces of this mode of origin may be seen in much later stages, and fig. 55 shows how the sporogenous tissue may still be recognized as composed of two parts, which are referable to the two initial archesporial cells. These sporangia have not been followed out into further detail. It may be mentioned, however, that seven or more initials are to be seen in the tangential section of a young sporangium. When the development of the sporangium in *L. alpinum* and *L. clavatum* has been described it will be seen that *L. inundatum* occupies an intermediate position between the more massive type and that of *L. Selago,* both as regards the mature form and also in respect of the earlier stages of development of the sporangium. It will subsequently be shown also that this mode of origin of the sporangium in *L. inundatum* approaches more nearly to that in certain species of *Selaginella* than any others which have been examined.

At the base of the strobilus of this species, where the gradual transition takes place from the sterile foliage leaf to the sporophyll, completely arrested sporangia are often found in the axils of the leaves. Passing upwards from these to the typical part of the strobilus a gradual passage to the typical sporangium may be traced (see p. 535).

L. clavatum. L.

The sporangium of this species is somewhat distinct from those which have already been described (figs. 92, *t*–*x*). Instead of the stalk being relatively thin, it is very short and massive in *L. clavatum,* while the sporogenous tissue forms a strongly-curved and rather less bulky zone, which fits immediately over the sub-archesporial pad ; this is here very massive, and, as seen in tangential section (fig. 92, *u*), projects far up into the sporangium : it has, moreover, this peculiarity, observed in no other species of *Lycopodium,* that its outline is distinctly convex in the radial section (fig. 92, *t*), and may even sometimes extend, as the sporangium becomes matured, into irregular processes, which project into the developing mass of spores ; in this we probably see a means of more ready transfer of nutritive materials from the base of the sporangium into the very large mass of spores. This character will be found of value when we come to compare it with the sporangia of *Lepidodendron.*

The sporangia are exceedingly well protected during their early phases. This may be gathered from figs. 92, *u*, *v*, *w*, in which it will be seen that the leaves closely invest the sporangia on all sides ; it is, moreover, to be remembered that these drawings are not made from the living specimen, but from such as have been treated with various hardening agents which would cause shrinkage ; it is probable that in the living state the chinks between these would be still smaller than as shown in the drawings. So close an investment is in broad contrast to the insufficient protection of the sporangia in *L. dichotomum*, *Selago*, and other species.

The sporangium of *L. clavatum* has been the subject of developmental study by SADEBECK (SCHENK'S 'Handbuch,' vol. 1, p. 313), who has figured various phases of its growth as seen in radial section ; but tangential and transverse sections are not mentioned by him. In the interpretation of the radial sections he has obviously been influenced by GOEBEL'S paper ('Bot. Zeit.' 1880) so often referred to in this memoir ; notwithstanding his working on a different species from GOEBEL, he still professes to a correspondence in results, so far that he refers the sporogenous tissue of *L. clavatum* to a single hypodermal cell as seen in radial section. This account is widely divergent from the results which I have obtained, and verified by comparison of radial, tangential, and transverse sections of sporangia in various stages of development. The difference lies in the recognition of the limits of the archesporial tissue ; now it is only by comparison of sections of sporangia of various ages cut in different directions that reliable views can be obtained on the recognition of the archesporium ; the mere distinctive qualities of the protoplasm and wall are not sufficiently defined in the earliest stages to make it possible to recognize the limits of the archesporium with certainty by their means. If, however, a comparison be made between his drawings and those which illustrate the description which I am about to give, it will be seen that SADEBECK'S drawings of the cell-net were more reliable than his recognition of the archesporium.

The sporangium, in this species, arises first as a broad flat growth on the surface of the sporophyll. A radial section through one which has just begun to undergo the characteristic cell-divisions shows hardly the slightest convexity of the surface (fig. 56); the part where the sporangium is to be formed is occupied by regularly arranged superficial cells, rather deeper than they are wide; in these, periclinal divisions begin to appear, of which but one is seen in fig. 56; but in fig. 57 two such divisions are already complete, and in a slightly older sporangium, shown in fig. 58, there are three. This is, in fact, the common number of such divisions in the young sporangium as seen in radial section, and a comparison of a large number of sections, both at these early stages, and also older, leads clearly to the conclusion that the sporogenous tissue is not referable in its origin to one cell as seen in radial section, but usually to three. A careful comparison of figs. 56, 57, 58 clearly shows that the periclinal divisions appear independently in the three superficial cells. The outer cells thus defined form the wall of the sporangium; they divide first anticlinally, as the sporangium gradually enlarges (fig. 58), then also by periclinal walls (fig. 59), while the inner layer thus produced again divides periclinally (fig. 60); the result is as in *L. Selago,* &c., and the three resulting layers develop further in virtually the same way. The three inner cells (fig. 58), undergoing repeated divisions, together form the sporogenous mass (fig. 59, shaded), and it is often possible, even in radial sections of advanced stages of development, to distinguish these cell-groups, resulting from the division of the three parent cells. It is to be noted that these cell-groups are of unequal size, the smallest being usually that most remote from the stem (compare figs. 58, 59, 60). The sub-archesporial tissue is rather irregular in its further development; sometimes the limit between it and the sporogenous tissue is even and regular (fig. 59); it often becomes convex as maturity approaches (fig. 92, *t*), but it is not unfrequently very irregular, as is the case in fig. 60, where there are sharp angles in the line of limitation of the sporogenous tissue, these angles coinciding with the limits of the masses of tissue derived from the three parent cells. In some sporangia this tissue even grows upwards as projecting teeth, which, as the sporogenous cells separate from one another and become rounded off, force them aside, and proceed a considerable distance into the mass. This point is of interest for comparison with *Lepidostrobus* (see below, p. 526).

Returning to early phases again, abnormal cell-divisions are occasionally met with; these are not to be ascribed to oblique cutting of the sections, for the presence of a continuous vascular strand has in each case been taken as a criterion of the section being truly in the radial plane. In such sections it may occasionally be seen that the superficial cells divide again, very early, by periclinal walls; the inner cells thus formed (*o, o,* figs. 61, 62) are believed to be added to the sporogenous tissue, but this has not been distinctly proved. In view of the fact that such additions to the sporogenous tissue are constant in *Equisetum,* as above described, there can be no *à priori* objection to this view, which will also gain further strength from facts to be described in the case of *Isoetes.*

Neither GOEBEL nor SADEBECK gives details of tangential sections; both leave the question open as to the number of cells of which the archesporium is composed, or, indeed, whether all may not be referable to a single parent. SADEBECK (note, *loc. cit.*, p. 313) remarks that this question is unimportant; to this view I cannot agree.

Tangential sections of sporophylls of about the same age as that shown in fig. 56 solve the question at once (fig. 63); here the same regularly disposed superficial cells are found, as have been noted in the radial sections; some of these have already divided by periclinal walls, others are still undivided. It is plain from such a case as this that a large number of parent cells divide thus to form the internal archesporium and external cells of the wall, and in fig. 63 the number appears to be at least twelve. In fig. 64 the archesporium is clearly defined, while the cells of it have already undergone further divisions, and the whole sporogenous mass is beginning to assume the characteristic form already noted. The cells of the wall have not yet begun to divide in a periclinal manner, but in fig. 65 a still more advanced stage is shown, and a comparison of this with fig. 60 will be found to agree in essential points, though the latter was taken from a slightly older sporangium.

The tangential sections show from the first that the lower limit of the archesporium is not a regular line; as the sporogenous tissue grows older the limit becomes more irregular, owing to the frequent growth upwards of the sub-archesporial tissue, which extends as more or less projecting processes between the sporogenous cells; these processes are irregular both in occurrence and form. Fig. 66 shows one of these in a sporangium in which the spore-mother-cells have not yet separated, or divided into tetrads; while in fig. 67 a later stage is seen, after the tetrad division; the cells of the processes are thus beginning to be disorganized, their function as purveyors of nourishment being almost complete. These figures will supply material for interesting comparisons with similar developments in certain specimens of *Lepidostrobus* and in *Isoetes* (see p. 526, 532).

Turning now to transverse sections, we shall seek in them for some corroboration of the results acquired from study of the radial and tangential. It is to be remembered, however, that the sporangium is a curved body, and, accordingly, that if the central part of the sporangium be cut in a tangential plane, the parts right and left of it will necessarily be cut obliquely.

That the sporangium is a broad and massive structure is borne out by a superficial section, such as that shown in fig. 68, which exhibits the external cell-net. A section of a similar sporangium at a lower level will traverse the sporogenous tissue, as in fig. 69, and if we imagine this cut in a plane (x, x), the result would be nearly similar to that shown in fig. 58, the heavier lines in both cases indicating the limits of the original archesporial cells. Again, at a later stage, the sporogenous tissue is shown in fig. 70; the drawing here stops short at the median plane, and it is not difficult to see how this will coincide in all essential points with what is seen in radial section in fig. 59. It will be unnecessary to pursue these comparisons further into detail, the figures should sufficiently explain themselves to those who are accustomed to such comparisons.

The strobilus of *L. clavatum* is clearly defined from the vegetative region; it is borne on a long, upright stalk, which is covered by small, closely-appressed leaves. If sections of the base of the strobilus be examined, imperfect sporangia may frequently be found attached to the lower leaves, and corresponding in position, though not in ultimate development, to normal sporangia. Similar imperfect sporangia also occur at the upper limit of the strobilus, while the uppermost leaves are completely sterile.

Comparison of details of sporangial development in L. clavatum, *and other species, especially* L. Selago.

1. The sporangium is similar in position and in general form to that of *L. Selago*, but its body is more strongly curved.
2. The archesporium here consists of *three rows of cells*, each row being composed of a large number (about 12) of cells; thus the extent of the archesporium is much greater than in *L. Selago*: occasional additions to it seem to be made by cells cut off periclinally from the superficial cell at an early stage.
3. The tapetum is similar in origin to that in *L. Selago.*
4. The sub-archesporial pad is much more developed, and is at times extended as processes of tissue which penetrate the sporogenous mass for a short distance.
5. The stalk of the sporangium is much thicker and shorter than in *L. Selago.*
6. Arrested sporangia are frequently present, and may be found either at the base or the apex of the strobilus.

6. *L. inundatum* may be looked upon as an intermediate link between the type of sporangium of *L. Selago* and that of *L. clavatum*, both as regards form of the sporangium and complexity of the archesporium.

L. alpinum. L.

This species shows great similarity to *L. clavatum*, both as regards the form of the sporangium and the very complete protection of it while young by the adjoining sporophylls (figs. 92, *q*, *r*, *s*); but the stalk of the sporangium is not quite so short, nor is the sporogenous part so strongly curved, while the sub-archesporial pad does not project so convexly, as seen in the radial section (fig. *q*).

The sporangium here also originates as a very broad outgrowth, extending from the first over numerous cells of the radial section (figs. 71 and 72). At least three cells in each radial section are involved in the origin of the archesporium (figs. 73, 74), but the position of the successive divisions does not appear to be strictly fixed, so that it is difficult to recognize the limits of the archesporium in very early stages such as those in figs. 71 and 72. Occasionally here also further periclinal divisions appear in the superficial cells, by which subsequent additions may be made in the archesporial tissues, as in *Equisetum.* The cells marked (x) in fig. 74 are believed to be thus added on to the archesporium; this is, however, unusual.

The further development proceeds in essential points as in *L. clavatum*, and it would hardly have been necessary to illustrate it by fig. 75, had it not been that the vascular bundle showed, in the one case figured, a slight extension upwards toward the sporangium. I do not wish to make more of this than the facts warrant, but the drawing is a faithful representation of what was seen in this exceptional case. It is a matter for remark that these sporangia of *Lycopodium*, though they are of so considerable size, have no vascular supply; in the whole genus this one case is the only trace I have seen of any extension of the vascular system in the direction of the sporangium.

Tangential sections show that the number of archesporial cells is large; and fig. 76, which is at a phase of development intermediate between those of figs. 63 and 64 of *L. clavatum*, shows very beautifully that the number of these is twelve. The limit of the sub-archesporial pad often becomes irregular as the development proceeds; even in an early condition (fig. 76) it is far from being a straight line, but it becomes more irregular with age (fig. 77), the cells of this sterile tissue forcing their way upwards into the sporogenous tissue, and occasionally forming multicellular processes. The development of it, however, is not carried to so great an extent as has been already noted in *L. clavatum.*

Beyond the facts now described, the structure of the sporangium of *L. alpinum* calls for no further remark; it is obviously similar, in its main aspects, to that of *L. clavatum*, notwithstanding the rather marked difference of external appearance of the two species.

Abortive sporangia are commonly found in this species, both at the upper and lower limits of the strobilus; they show, perhaps better than in any other species, the gradual steps of transition from the fully mature to the completely abortive condition.

SELAGINELLA.

In the species of *Selaginella* which have been examined similar abortive sporangia are found at the base of the strobilus; the larger the number of examples of this that are disclosed, the more important does it become that some adequate explanation of the phenomenon should be given. (See below, p. 535.)

Turning to the development of the normal sporangia in *Selaginella*, the most exact account hitherto given is that by GOEBEL ('Bot. Zeit.,' 1881, p. 697, &c.): he remarks on the difficulty of following the details of segmentation, owing to the small size of the cells; this may account for the divergence of my results from those of GOEBEL, and it should make one cautious in making definite statements on minute details.

As regards the position of the sporangium of *Selaginella,* I am able to endorse GOEBEL'S statement (*loc. cit.*, p. 697) as to the position of the sporangium in *S. spinosa,* P. B. (= *S. spinulosa,* A. Br. = *S. selaginoides,* LINK): it originates from a group of cells of the axis which lie at the axil of the sporophyll (figs. 80–86), and immediately above those which give rise to the leaf itself. In *S. Martensii,* however (fig. 78), I find the sporangium to originate on the axis, distinctly above the sporophyll. The mere fact that there is variety within the genus in this much discussed and greatly overrated character, should show sufficiently that, however interesting its morphological bearings may be, it is not a point of much systematic importance.

The sporangium of *S. spinosa* is eusporangiate, arising from a number of cells, as seen in radial section; it is possible, however, that these may all be ultimately referable in origin to a single cell (compare figs. 80, 81, 82). The young sporangium may thus be recognized in the radial section as consisting of three cells, which early undergo periclinal divisions to form three cell-rows (figs. 80, 82); these may occasionally show anticlinal divisions also (figs. 81, 83). GOEBEL now describes how the middle row of cells grows more strongly than the peripheral ones, while the hypodermal cell of this series forms the archesporium;* thus, according to his description, the sporogenous tissue in any radial section is referable to the subdivision of a single cell. I do not deny that this may sometimes be the case, but I have not been able to prove to my own satisfaction that it ever is so.

From many specimens which I have seen I find little evidence of the early preponderating growth of the middle row; it appears rather that the three rows grow about equally, while *sporogenous tissue originates from at least two of the rows of cells* above noted; for instance, in fig. 83, a continuous wall (x, x) divides the sporangium into almost equal halves; it is believed that both the cells shaded, though derived from different cell-rows, are archesporial cells; a comparison of drawings of sporangia in older states shows that a continuous wall, occupying an almost median position in the sporangium, is not uncommon (figs. 84, 87, walls marked x), and it is believed to correspond to the wall similarly marked in the younger sporangia (figs. 80, 82). If this be so, then, in figs. 83 to 87, the shaded mass of cells must have been derived from at least *two* of the rows of cells of the younger sporangium.

For confirmation of this result radial sections were also cut from *S. Martensii,* which species illustrates this point very clearly. The sporangium originates here from the axis, distinctly above the subtending leaf (fig. 78), as an outgrowth of at least two cells as seen in radial section; the wall dividing them occupies from the first a median position, and divides the sporangium into two equal halves; in this case a comparison of figs. 78 and 79 can leave little doubt that two cell-rows are involved in the formation of the archesporium.

It may be noted at once that a similar state of things is seen in *Lycopodium*

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* *Loc. cit.*, p. 698, and SCHENK'S 'Handbuch,' 111, p. 388.

inundatum (compare figs. 54, 55), and that, as regards the origin of the sporangium, *Selaginella* seems to correspond more nearly to that species than to any other *Lycopodium* which has been examined.

Tangential sections of sporangia corresponding in age to those shown in figs. 84–86, demonstrate a similar fan-like tracery to that seen in the sporangia of *Lycopodium.* I have not been able to define exactly the number of primary archesporial cells, owing to the great difficulty of obtaining exact tangential sections of very young sporangia. I believe, however, that the number is not less than three or four (fig. 88).

The further differentiation of the sporogenous tissue and of the tapetum may now be discussed. GOEBEL states (*loc. cit.,* p. 698) that the part of the tapetum which adjoins the outer wall is separated off from the archesporium, as distinguished from that of *Lycopodium,* which is derived from the cells of the wall. Though certainly a large part of the tapetum is so derived, I am not prepared to admit that this is its exclusive source, and find myself unable to endorse the account of the details as given by GOEBEL. Taking first *S. Martensii,* it will be noted that the two superficial cells of the sporangium in fig. 78 are relatively deep ; in fig. 79, which represents an older sporangium, they are relatively shallow, the cells immediately below them (*i, i*) would, according to GOEBEL'S description, be derived by division from the internal, not from the external cells, but the position of the walls, together with the less depth of the superficial cells in the older specimen, seem to indicate that they originate from division of the superficial cells. I venture to think that GOEBEL'S own fig. 14 ('Bot. Zeit.,' 1881, Plate 6) is quite open to the same interpretation, and that the cell marked (*t*) is the result of division from the next outer, and not from the next inner cell. An examination of numerous sections of sporangia of *S. spinosa* also strengthens the view that, at times, early periclinal division of the superficial cells may contribute to the internal tissue of the sporangium, though I have not found this point so clearly demonstrated in this species as in *S. Martensii.* My conclusion is, that the first periclinal division does not constantly define the archesporium, and thus separate the internal mass of the sporangium from the sporangial wall, but that, as observed with constancy in *Equisetum,* and occasionally in other plants (*L. clavatum* and *alpinum*), by periclinal divisions of the superficial cells additions may be subsequently made to the archesporium, but these additions are not constant.

Whatever may be the actual facts on the above point, there can be no doubt that after the archesporium has grown and undergone further segmentation, periclinal divisions take place in the peripheral cells of the resulting mass of tissue, these divisions separate off the tapetum from the sporogenous cells (figs. 87, 88, 89). Thus, as GOEBEL has already pointed out (*loc. cit.*, p. 698) the tapetum of *Selaginella* differs in its mode of origin from that of *Lycopodium,* but when we look back to the earlier phases, and recognize the periclinal divisions discussed in the preceding paragraph, the distinction of the two types appears to be not so deep a one as he described.

The further facts of differentiation of the sporangia, as mega- and micro-sporangia, are well known; but there is, I believe, no published figure of the early stage of differentiation of the megaspore-mother-cell from the rest; this is shown in fig. 91, as having undergone tetrad-division, and beginning to enlarge, while the other cells of the sporogenous mass remain undivided, lose their highly refractive contents, and become disorganized. It is hardly necessary to remark that here is a further example of a partial sterilization of the potential sporogenous tissue, and the tapetum of *Selaginella* is also another, since, though it is derived by segmentation from the sporogenous mass, its cells take no direct part in the formation of spores.

Summary of Results from Selaginella.

1. The sporangium is eusporangiate, and arises from the tissue of the axis, above the subtending leaf; the position varies in different species.
2. The origin of the sporangium is similar to that of *Lycopodium,* and especially resembles *L. inundatum,* to which species the mature sporangium also is similar in form.
3. Two primary archesporial cells are usually present in each radial section, and these are derived, as in *L. inundatum,* from segmentation of two distinct cell-rows; as seen in tangential section, the archesporium is referable to three or four such cell-rows.
4. The first periclinal divisions in these cell-rows do not always define the archesporium finally; subsequent periclinal divisions may result in addition to the central mass, as has been proved for *Equisetum;* but here the addition is less regular.
5. The tapetum results from tangential division of the outermost cells of the central mass; the greater part of it originates as described by GOEBEL.
6. The tapetum is thus a sterilized part of the potential sporogenous tissue; a further example of sterilization is seen in the megasporangium, where all the sporogenous cells are disorganized, excepting the one mother-cell of the megaspores.
7. Abortive sporangia are to be found at the base of the strobilus as in many species of *Lycopodium.*

LEPIDODENDRON.

The general characters of the sporangium in *Lepidodendron* are well known by the observations of R. BROWN, Sir JOSEPH HOOKER, WILLIAMSON, and others; a concise statement of their results will be found in SOLMS-LAUBACH'S 'Fossil Botany' (Engl. Ed., p. 232, &c.). It is to be noted, however, that the comparison with the sporangia of living forms has been limited, partly perhaps owing to the incomplete knowledge of the sporangia of modern Lycopods. The facts which have been collected and described in the preceding pages make it possible to draw the comparisons closer.

while observation will, at the same time, be more carefully directed to points of detail which have hitherto received but slight attention.

The magnificent silicified cones in the British Museum have supplied the most important material. I take this opportunity of thanking the Keeper of the Botanical Department, not only for giving the free use of the specimens, but for readily agreeing to my suggestions for cutting new sections of parts of these rare fossils.

Lepidostrobus Brownii, SCHPR.

The large specimen of this species purchased for the British Museum in 1843, is the best preserved which I have seen, probably the best that is known to science. It is possible in microscopic sections of the cone to study its parts with the same detail as those of a modern Lycopod, while, since the sections in the British Museum are cut in all three directions, transverse, radial, and tangential, a very satisfactory knowledge of the structure both of the axis and sporophylls, and also of the sporangia, may be acquired. The radial and transverse sections were made for R. BROWN, and his account of them will be found in the Linnean Transactions (vol. 20, p. 469, Plates 23 and 24). It is remarkable how little attention has been paid to this memoir, and to the fossil to which it relates; even SOLMS-LAUBACH dismisses it with few words, and with the quotation of two figures which do it but scant justice ('Fossil Botany,' Engl. Ed., p. 238, and figs. 25A and 25B).

The structure of the axis is not our subject here; I have given a description of certain details of it elsewhere ('Annals of Botany,' 1893); we are more nearly concerned with the sporophylls and sporangia. These are of great size; each sporangium, when mature, being over half an inch in length, more than three-sixteenths in width, and almost of equal depth. The sporangia are so placed that the longer axis runs in a radial direction; each is closely applied to the upper surface of the sporophyll throughout the greater part of its length, while the basal portion of the sporophyll is elongated so as to accommodate the large sporangium (compare R. BROWN'S Pl. 23, B, C, Pl. 24, B). I have not been able to observe any structure comparable to the ligule in this fossil.

The sporangia are filled with very numerous microspores, which were described and figured by R. BROWN. Turning to the wall of the sporangium, R. BROWN remarks (p. 471), that it "appears to be double; the outer layer being densely cellular and opaque, the inner less dense, of a lighter colour, and formed of cells but slightly elongated." A detailed examination of the sections shows that the wall consists of several layers of cells (fig. 93), of which the outermost consists of closely disposed prismatic cells, the walls of which were apparently much thickened; within this is a broad band of cells, consisting of four or more layers, with thin walls, and irregular, but compressed form; this wall is lined internally by an ill-defined band, which possibly represents the remains of the tapetum, and it directly adjoins the spores.

The interest of this rather complex structure depends upon comparison; among the various species of *Lycopodium* which have been examined, there are usually three layers of the wall, of which the innermost is the tapetum; but *L. dichotomum* is an exception, and it has been shown that in this species the wall is constructed in a manner very like that now described for *Lepidostrobus Brownii*, though the details of the outer layer are rather different. Again, a similar structure of the sporangial wall is found in the *Ophioglossaceæ*, a point noted by R. BROWN (*loc. cit.*, p. 471).

One of the most remarkable features in these sporangia is the existence of irregular processes which spring upwards from the floor of the sporangium, where it adjoins the sporophyll, and project a considerable distance into the cavity: they were noted *loc. cit.*, p. 471), and figured (Plate 24, fig. B), by R. BROWN, but appear to have entirely escaped the notice of subsequent writers. They are not scattered indiscriminately over the floor of the sporangium, but arise from a projecting ridge, which lies immediately above the single vascular bundle of the sporophyll, and follows its course almost the whole length of the sporangium; in transverse sections this ridge may be seen (fig. 94), but it is in tangential sections that it will be best recognized (figs. 95, 96), together with the processes of tissue which arise from it and radiate upwards into the cavity: it is obvious that the ridge corresponds to the mass of tissue which has been styled the "sub-archesporial pad" in describing the sporangia of *Lycopodium.* These process which thus arise from the sub-archesporial pad are irregular in outline and position; they consist of a parenchymatous tissue, which is directly continuous with the base of the sporangium (figs. 97, 98); the cellular structure, however, cannot always be recognized in the ultimate endings of the process, where they appear to have undergone considerable disorganization.

The question now presents itself, What is the real nature of these processes? Are they comparable to the trabeculæ of *Isoetes*, which are the result of partial sterilization of a potential archesporium, or are they merely outgrowths from the subarchesporial pad, such as those already described in certain species of *Lycopodium?* (compare *L. clavatum*, figs. 66 and 67; and *L. alpinum*, fig. 77). This question can only be decisively answered by observations of development, which can hardly be expected in fossils; there are, however, facts bearing on the point which may be acquired from the apical parts of this remarkable cone; it will be seen that in fig. 95, as the apex is approached, the sporangia are successively smaller; those close to the apex have been arrested in their growth, and appear to contain no spores; the cavity of the sporangium is, however, traversed by cellular processes, rising from the base, and extending upwards (figs. 99, 100); apparently these bands of sterile tissue extended to the upper wall of the sporangium, but I have been unable to establish beyond doubt the fact of a tissue-connection between them and the wall; had that been shown to exist, the correspondence between these and the sterile trabeculæ of *Isoetes* would have been demonstrated, and, from the appearance of some of the sections, I am inclined to the belief that this is their real nature; in the absence of such proof it may be held as a possible alternative view, that they are merely upgrowths of the subarchesporial pad, like those in certain species of *Lycopodium*, but on a larger scale, and that those upgrowths are specially large in the abortive sporangia; but I think the former view the more probable.

The second specimen of *L. Brownii*, from SCHIMPER'S collection, and now in the British Museum, has been figured by SCHIMPER ('Traité,' Plate LXII., figs. 13, 14). I have to thank the Keeper of the Botanical Department of the Natural History Museum for having this classical fossil cut in tangential section; the result is to demonstrate the presence of sterile trabeculæ similar to those seen in BROWN'S cone (fig. 102). From the enlarged subarchesporial pad processes of sterile tissue may be seen to arise, and project far into the sporogenous mass; but no evidence is to be found of the continuation of the trabeculæ outwards to the sporangial wall; it is, however, to be noted in this connection that the cone is not so well preserved as BROWN'S cone, and it does not include the apex.

It will be obvious, on comparison of RENAULT'S figures of *L. rouvillei* ('Cours de Bot. Foss.,' II., Plate 7, fig. 11), that M. RENAULT has observed in that species characters similar to those above described.

The presence of these sterile masses, whether they be true trabeculæ, or merely upgrowths of the subarchesporial pad, has its physiological interest. The sporangium is an unusually large one, and the spore-producing mass very bulky; the difficulties of supply of nourishment to so large a mass are obvious, and would be greatly diminished by processes of sterile tissue, such as these, extending far into the mass. It is further to be noted that they are inserted near to the vascular bundle of the sporophyll, and radiate from it; there can be little doubt that their function is the ready conveyance of nutrition to the developing mass of spores. Whether we can regard them as also performing a mechanical function, in supporting the roof of the sporangium in early stages, depends upon the question of the tissue connection, which I have been unable to decide.

Lastly, a formal comparison may be drawn between the sporangium of *Lycopodium* and that of *Lepidodendron;* at first sight the correspondence does not seem a close one. Comparing the tangential sections, it will be seen that fig. 96 of *Lepidodendron* is not unlike fig. 92R of *L. alpinum*, as regards the form of the sporangium, its relation to the sporophyll, and the subarchesporial pad, with its irregular upward projections. The radial and transverse sections, however, differ greatly, for the sporangium of *Lepidodendron* is extended radially, while that of *Lycopodium* is radially compressed; but, after all, this is only a difference on a larger scale, though similar in kind to that already observed between the different living species of *Lycopodium;* I have shown that in some species (*e.g.*, *L. Selago*) the archesporium is represented in radial section by a single cell, while in others (*e.g.*, *L. alpinum* or *L. clavatum*) it is represented usually by three. Why should the limit be three? Why not thirty-three?

Probably some such extravagant extension of the archesporium in a radial direction existed in *Lepidodendron*, and its sporangium appears to be of the ordinary Lycopodinous type, but extended greatly in a radial direction, the result being a much greater possible production of spores, accompanied by risks for their proper nourishment, while there are special developments to meet those risks, and to provide for the nutrition of the developing spores.

Other Lepidodendra.

It has long been recognized that all *Lepidostrobi* do not correspond in the details of their sporangia; there is a type distinct from *L. Brownii*, which has already been figured and described by WILLIAMSON (Memoir III., 'Phil. Trans.,' vol. 162, 1872, p. 28, Plate 12, figs. 24, 25). This type appears also to be that which chiefly engaged the attention of Sir J. HOOKER in his memoir in the publications of the Geological Survey of Great Britain, vol. 11, p. 440. Sporophylls with their sporangia similar to those figured by these authors are shown as cut in tangential section in fig. 101, which is photographed from a specimen of my own, from Hough Hill, Stalybridge, supplied by Mr. Lomax. I find the details to correspond to Professor WILLIAMSON'S description (p. 295); the wall of the sporangium consists for the most part of only a single layer of hard, prismatic cells, and is, thus, simple in structure as compared with the relatively thick wall of *L. Brownii.* The sub-archesporial pad projects only very slightly into the cavity of the sporangium, but from it arises, usually in a median position, a dark line, readily seen in the photograph, and represented in WILLIAMSON'S figs. 23, 24, 25. Sometimes there is evidence of its bifurcating at the middle of the sporangium, while in other cases it appears of less regular form and position. Minute examination of the upper part of it does not disclose any definite cell-structure. Comparison with the mature microsporangia of *Isoetes* makes it almost certain that it represents a process of sterile tissue, for in the mature microsporangia of that plant the trabeculæ, which are of cellular construction, become so shrivelled that the individual cells are unrecognizable, the result being closely similar to what is seen in sporangia of *Lepidostrobus*; moreover, an examination of the base of the dark processes in *Lepidostrobus* shows, at times, evidence of distinct cells (fig. 102). These processes thus appear to correspond essentially to those already described in *L. Brownii*, though they are less numerous as seen in tangential section. In a transverse section of the strobilus, thus traversing the whole length of the sporangium, the brown line appears sometimes as a single continuous plate (compare WILLIAMSON'S Plate 44, fig. 23), occupying the median plane in each sporangium. WILLIAMSON describes each as being "coextensive with the entire length of the sporangium." In a transverse section of *Lepidostrobus*, from Hough Hill, Stalybridge, supplied to me by Mr. LOMAX, I find the median plate very much as described by WILLIAMSON, though not extending the whole length of the sporangium (fig. 132). In another transverse section of *Lepidostrobus*, also supplied to me by Mr. LOMAX, from Dulesgate, I find two such brown lines, which run almost parallel for a considerable distance, while a third less continuous line is seen to run for a short distance in a position between them (fig. 133). Thus we see that in different specimens of *Lepidodendron* these processes are of variable form, being peg-like upgrowths, or trabeculæ in *L. Brownii*, while in those last described they take the form of continuous plates. The resemblance of these plates to partial septa cannot be overlooked, and this inconstancy of character is a fact which will have its bearing on our general argument.

The question whether these processes are to be looked upon as sub-archesporial in origin, or as the result of a partial sterilization of the archesporium itself, must here also remain uncertain, in default of developmental data, which are necessary for deciding such a question. I think, however, that comparisons, on the one hand with *L. Brownii*, and on the other with *Isoetes*, justify the conclusion that in these simpler sporangia of *Lepidodendron*, also, the brown lines represent sterile tissue, which in the course of development of the spores has become disorganized, and the cells shrivelled out of shape.

Summary of Results from Lepidodendron.

1. The general arrangement of parts of the strobilus of *Lepidodendron* corresponds to that of *Lycopodium*.

2. The sporangium is greatly extended in a radial direction, and is to be looked upon as an extreme case of that radial widening of the sporangium which is seen in much less degree in *L. clavatum* or *L. alpinum*.

3. There are two types of sporangia of *Lepidodendron*: (*a*) that of *L. Brownii* in which the sporangial wall is several layers of cells in thickness, and the cavity traversed by rod-like masses of sterile tissue (trabeculæ); (*b*) those in which the wall consists of a single layer when mature, and the cavity traversed by one or more irregular plates of sterile tissue.

4. These sterile trabeculæ, or plates, arise from the sub-archesporial pad, and from early states of development seen in *L. Brownii* it seems probable that they are similar in their origin to the trabeculæ of *Isoetes*, but this has not been proved.

5. The physiological importance of these sterile processes projecting into the cavity of the sporangium is probably to forward supplies of nourishment more readily from the vascular bundle, above which they spring, to the mass of developing spores; they may also have served a mechanical purpose.

ISOETES LACUSTRIS, L.

The genus *Isoetes* presents points of special interest in connection with the investigation upon which we are engaged. Though the development of the sporangia has been most carefully and successfully wrought out by Professor GOEBEL ('Bot. Zeit.,' 1880, p. 564), still there are certain details to be added, which are the outcome of my work in verification of his results.

Before describing these, a few preliminary remarks will not be out of place. The question of the systematic position of *Isoetes* has recently been re-opened by Professor VINES ('Annals of Botany,' vol. 2, p. 117), and on various comparative grounds he holds that *Isoetes* should be included in the Filicineæ, having more special affinities with the Eusporangiate Ferns. He still admits, however, that "there is some affinity between *Isoetes* and the Lycopodinæ" (*loc. cit.*, p. 123). I think that the comparison with *Lepidodendron*, rather than with modern Lycopods, greatly strengthens the affinity with the Lycopodinæ, more especially the comparison of their sporangia. I have already stated in the introductory pages of this memoir that I attach greater weight to the characters of the sporangium than to those of other parts of the sporophyte, and accordingly I am disposed to recognize a nearer affinity of *Isoetes* to the Lycopodinæ than Professor VINES would do. The description of details now to be given will, I think, justify this view.

The sporangium of *Isoetes* obviously corresponds in position to that of *Lycopodium*, though it differs from it in form. It arises from the upper surface of the sporophyll, at a point between the ligule and the base of the leaf. GOEBEL ascribes the sporangium to a group of cells, which extend, and divide by periclinal walls, and he continues, that according to his observations on *Isoetes lacustris*, it is usually the three uppermost layers of cells which give rise to the sporangium. For purposes of comparison with the Lycopodinæ, it is desirable to trace the origin of the sporangium back to earlier phases than that where it consists of three layers of cells. The stage shown in fig. 104 will serve as our starting point; the superficial series of cells lying at the upper surface of the leaf, between the ligule (*l*), and the base, here represent the parent cells of the sporangial wall and of the archesporium; the cell (V.), which gives rise subsequently to the "velum," must, however, be excepted. These cells divide by periclinal walls, and also anticlinally, to form two layers; the outer contributes the wall of the sporangium, the inner is the archesporium (fig. 105, shaded). As in the case of other sporangia, so here also the question arises whether the first periclinal division of the superficial cells clearly and finally divides the wall from the archesporium, or whether further periclinal divisions in the former contribute additions to the latter. We have already seen that such additions are made with constancy in *Equisetum*, while occasional and irregular periclinal divisions appear also in young sporangia of *Lycopodium* and *Selaginella*. GOEBEL has noticed such divisions occurring in the sporangium of *Isoetes* (SCHENK'S 'Handbuch,' 3, p. 92), and remarks that this doubling of the layer of the wall is very common, though not so regular as in *Lycopodium*; evidently he regards it merely as a division of the wall of the sporangium into two layers. I also find periclinal division of superficial cells, after the first formation of the archesporium, to be not uncommon; it is to be noted, however, that such divisions occur *at very early stages* in the development of the sporangium; their common occurrence then (figs. 106-108), and the much less common appearance of the doubling of the superficial layer of the wall at older stages (such as that shown in fig. 109), make it seem probable that the inner cells thus produced are contributed to the sporogenous mass. It is difficult to bring forward definite proof on this point, since the occurrence of such divisions is less regular than in *Equisetum.* A comparison of figs. 106–108, however, makes it appear extremely probable that the cells marked (×) in them are actually such additions to the sporogenous tissue, proceeding from a second periclinal division of certain of the superficial cells.

Be this as it may, the result of the segmentation is normally the formation of a superficial layer of cells forming the wall, while the subjacent cells, at first a simple row, become again divided by both periclinal and anticlinal walls, so as to constitute a continuous band several layers of cells in thickness (compare fig. 105 with figs. 106–108, and again with fig. 109). Below the archesporium a mass of tissue is found, intervening between it and the vascular bundle; as the sporangium grows this increases greatly in bulk, and forms the subarchesporial pad. It is to be noted that the sporangium does not extend the whole distance from the ligule to the base of the frond; the cell marked V (fig. 104) develops into the velum which intervenes between the ligule and the sporangium; also towards the base of the sporangium, a greater or less interval of sterile tissue is present from the first (figs. 105–109).

A comparison may now be drawn between the earliest stage of the sporangium of *Isoetes* (fig. 104) and that of *Lycopodium;* in certain species of the latter it has been shown that the sporangium is referable in its origin to a single cell as seen in radial section, and that a single archesporial cell is at a rather later stage disclosed in such sections (*L. Selago*, &c.). In another species (*L. inundatum*) the sporogenous tissue is referable to two cells as seen in radial section, while in others (*L. clavatum* and *L. alpinum*) the radial section traverses three original parent cells, all of which contribute to the sporogenous tissue. In *Isoëtes lacustris* the whole plant may be regarded as a strobilus; most of its leaves are sporophylls; when one of these is cut in radial section the position of the sporangium relatively to it is very similar to that of the corresponding parts in *Lycopodium*, but a larger number of ultimate parent cells take part in forming the sporangium, the number traversed by the radial section being about four or five; this difference is, however, in accordance with the hemispherical form of the mature sporangium. The result of the earlier segmentation is, as in *Lycopodium*, the formation of a continuous sporogenous mass, protected by a simple outer wall. A comparison of figs. 104–106 of *Isoetes* with figs. 56–58 of *L. clavatum*, and with figs. 72–74 of *L. alpinum*, will show how close is the similarity of first origin of the sporangia in these plants.

GOEBEL has already traced the differentiation of the *potential archesporium* of *Isoetes* to form, on the one hand the sterile trabeculæ and the tapetum, and, on the other, the megaspores or microspores. I may be excused for dwelling again upon this point since it provides a most important link in the chain of my argument. In fig. 109 the potential archesporium of a microsporangium is shown, of very considerable extent, but still undifferentiated; it enlarges further, and the cells show further divisions, the tissue meanwhile undergoing the differentiation described by **Goebel** ('Bot. Zeit.,' 1880, p. 565) to form the sterile trabeculæ (*tr.tr.*, fig. 110), and the fertile sporogenous masses (*sp.*, fig. 110); a layer of cells adjoining the wall of the sporangium is meanwhile divided off, and may be recognized as the tapetum (*t.*, fig. 110); this layer very soon divides periclinally into two.

Similar results are naturally to be obtained from transverse sections (fig. 111); in these the trabeculæ are seen radiating, as it were, from the slightly convex, subarchesporial pad, which intervenes between the sporogenous tissue and the vascular bundle of the sporophyll. This figure is added for purposes of comparison with *Lycopodium*, and, if we refer back to fig. 43 of *L. Selago* or fig. 64 of *L. clavatum*, the closeness of the similarity between them will be sufficiently plain. The potential archesporium of *Isoetes* clearly corresponds to the curved sporogenous mass of *Lycopodium*, the chief difference lying in the differentiation of the former into sterile trabeculæ and sporogenous masses. In fact, if we imagine a heterosporous Lycopod with its sporangium widened out radially, and its enlarged sporogenous mass partly sterilized so as to form trabeculæ, the result would be practically what is seen in *Isoetes lacustris*.

It is often wrongly assumed that the sporangia of *Isoetes* are actually partitioned, and some of the published drawings, if not corrected by description, support this error. The trabeculæ are not partitions, but, as their name implies, rods of tissue which radiate upwards from the subarchesporial pad; they are frequently very irregular both in number and form; though, in our figs. 110 and 111, more regular examples have been chosen, the specimen drawn as fig. 112 will sufficiently show such irregular branchings as may occur, while the structure of them is displayed more in detail in fig. 113; here the spore-mother-cells have separated from one another and rounded off: the tissues forming the trabeculæ have differentiated into a superficial tapetum, here shaded, and central parts which remain after the tapetum becomes disorganized. As the sporangia approach maturity all that remains of the trabeculæ is the shrivelled central part, from which, as the spores ripen, the cell contents are abstracted, so that even the cell-structure is difficult to make out (fig. 115). In this state a comparison may be made with what has already been seen in *Lepidodendron;* if fig. 115 of *Isoetes* be put side by side with fig. 102 of *Lepidodendron*, the similarity is excessively striking. I think the conclusion may fairly be drawn that the processes observed in the sporangium of *Lepidodendron* are essentially similar to the trabeculæ of *Isoetes*, though we note differences of detail in their distribution in the two cases, and though we are not in a position to state that their development in *Lepidodendron* is like that in *Isoetes*.

When further the form of the sporangium in the two cases is compared, especially the large area and radial extension, it may be concluded that *Lepidodendron* presents characters of the sporangium more closely similar to those of *Isoetes* than does any one of the living Lycopods; this comparison materially strengthens the affinity of *Isoetes* with the Lycopodinæ.

The description above given relates both in *Lepidodendron* and in *Isoetes* to the microsporangium; as regards the megasporangium of the latter plant, I have nothing material to add to the excellent description of GOEBEL, beyond saying that I am able to confirm his results; the differentiation of the potential archesporium into sterile trabeculæ and fertile spore-mother-cells is clearly similar to that in the microsporangium. In both cases a partial sterilization of the potential archesporium is to be traced.

Summary of Results from Study of Isoetes.

(1.) The sporangium of *Isoetes* corresponds in position on the sporophyll to that of the Lycopods, in form it compares more nearly with *Lepidodendron.*

(2.) It originates from superficial cells of the basal part of the sporophyll, which divide periclinally and anticlinally, forming the superficial wall, and subjacent archesporium.

(3.) Additions appear to be sometimes made to the sporogenous tissue by subsequent periclinal divisions of superficial cells, as in *Equisetum,* and occasionally in *Selaginella* and *Lycopodium.*

(4.) The sporogenous tissue is later differentiated into sterile trabeculæ and spore-producing masses; the former are derived by sterilization of potential archesporial cells.

(5.) The trabeculæ resemble in structure and function those of *Lepidostrobus Brownii.*

THEORETICAL CONSIDERATION OF THE RESULTS ACQUIRED BY STUDY OF THE LIVING LYCOPODS, LEPIDODENDRON AND ISOETES.

We have now examined a considerable number of forms, living and fossil, which are more or less closely allied to one another, and may venture upon some theoretical conclusions which may be drawn from the study of them. It is, meanwhile, to be remembered that such organisms as these which have been studied are generally believed to represent very ancient types; this may be concluded both on comparative and on palæontological grounds.

It was assumed at the outset that, other things being equal, it is a distinct advantage to an organism to increase the number of spores produced; we may specially examine these plants from this point of view, and consider how they severally illustrate the balance of two conflicting factors, viz., (1) the advantage of increased spore-production, (2) the risk of damage, and the difficulty of nutrition of large masses of sporogenous tissue, especially at the period of the tetrad-division, when the cells of the sporogenous mass do not form a coherent and firm tissue.

For reasons above stated (p. 506), *Phylloglossum* is regarded as a primitive, rather than a reduced form; its small and comparatively simple strobilus is, on our working hypothesis, the counterpart of a sporogonial head, which in this plant is separated sharply by the intercalary growth of the axis, from the protocorm with its protophylls. The sporangium of *Phylloglossum* is not in any sense an extreme type, either as regards size, or peculiarity of form; it seems not improbable that it may represent something like the original Lycopodinous sporangium, though there is no definite proof that it is the original type.

Supposing it to be so, and its whole strobilus to be really a primitive type, let us imagine in what ways the increase in spore-production might be effected, and then inquire whether any of these are exemplified by plants before us. We may imagine that the spore-production might be increased:—

(1.) By lengthening and even branching of the strobilus, and increase of the number of sporophylls and sporangia produced in ordinary sequence.

(2.) By increase in size of the individual sporangium.

(3.) By formation of adventitious sporangia in places where they were not previously produced.

We will consider each of these separately.

(3.) The third head may be at once dismissed; within the Lycopods and allied forms which we are considering, no adventitious sporangia have been observed.

1. Lengthening and branching of the strobilus has probably been a potent factor in the production of the large Lycopodinous forms from a simpler ancestry;* whether or not *Phylloglossum* really represents, or is at all like such ancestors, it is not to be doubted that earlier ancestors were simpler than they, and it has been already remarked that the structure and development of its strobilus show facts not incompatible with the recognition of its strobilus as the counterpart of a sporogonial head. It is not difficult to realize how a strobilus, gifted with continued apical growth, and a power of branching (as is foreshadowed in the sporangia of some Bryophytes as a rare abnormality, and also is seen in fig. 23 in *Phylloglossum*) might form a larger number of sporangia than its predecessors, and the total output of spores be thus increased. But to nourish the increasing number of spores, increased vegetative development will be needed: this need is not met in the Lycopods by increase of the vegetative development of the sexual, but of the non-sexual generation, and on comparative grounds it appears to me probable that an increased assimilative power was acquired by them in the following most interesting way. It is a familiar fact that certain species of *Lycopodium* have alternating sterile and fertile zones; examining the limits of the fertile zones, the sporangia, though present, are abortive; in the presence of these arrested sporangia I believe that we have evidence that the whole sequence of sterile and fertile zones is the result of partial sterilization of a primitive strobilus, all potentially fertile, but of which parts are sterilized, and carry on merely

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* See footnote, p. 484.

a vegetative function; the evidence of its potential fertility is to be found in the sporangia present in the axils of many of the vegetative leaves, though arrested in their development at a very early stage (*e.g.*, in *L. Selago, hippuris, dichotomum, carinatum*). In such species there is thus seen a primitive and incomplete differentiation of vegetative from sporogenous parts, and I see no improbability, but rather all evidence in favour of the view that the former are the result of sterilization of the latter. The physiological advantage is too obvious to need lengthy explanation, while, as the apex of the axis in these species retains its power of continued growth, the production of spores may be carried on without definite limit.

In other species the differentiation of the sterile and fertile zones is more complete, the latter appearing as clearly defined strobili (*e.g.*, *L. alpinum, clavatum; Selaginella Martensii, spinosa*). It has been repeatedly noted in the above pages that arrested sporangia are present at the base of the strobilus of such plants, they are also found at the apex. In the latter position they would be generally accepted as potential sporangia, arrested owing to insufficient supply of nourishment. I now suggest that the arrested sporangia at the base of the strobilus are to be explained in the same way, though they bridge over the limit between the sporophyll and the true foliage leaf. The correlation of growth is often very marked, *e.g.*, in *L. phlegmaria*, where the foliage leaves are relatively large, while the sporophylls are small: such forms might be regarded as those most advanced in point of differentiation.

I see no other way of explaining the presence of these abortive sporangia at the base of the strobilus, unless they be accepted as "prophetic germs," a suggestion which will not readily commend itself. And thus the general conclusion may be approached, which would well explain the facts, though it must only be held as an hypothesis, viz., *that, exclusive of the protocorm and protophylls, the plant of Lycopodium or of Selaginella may be looked upon as the result of elaboration of a strobilus by continued apical growth and branching;* that parts of the strobilus (usually the basal part, but sometimes alternating zones) became sterilized, the sporangia arrested, or entirely aborted, and these parts carry on the assimilating function, and supply nourishment to the residuary, fertile portions; these, in modern Lycopodia, appearing as the recurring fertile zones or as distinct strobili. Briefly put, *we see in Lycopodium evidence that the ordinary foliage leaf is a sterilized sporophyll.*

There is, I think, no inherent improbability in this theory, while it explains the presence of the arrested sporangia, which would otherwise be unintelligible. We may now picture to ourselves how, from a simple form, such as *Phylloglossum*, the larger Lycopods may have arisen by elongation and branching of the strobilus, and increase in number of sporophylls and sporangia, and, further, by partial sterilization of the strobilus.

As an objection to this theory it may be urged that it implies an antithesis between the protophylls and the ordinary vegetative leaves; that antithesis is, however, sufficiently clear in *Phylloglossum*, which, on other grounds, is marked out as being probably a primitive type of Lycopod. I do not wish, however, to press this antithesis too far; if we keep in view, for purposes of comparison, the case of the Bryophyta, it will be remembered that the distinction between the seta and the capsule is not always a very distinct one, and this may also have been the case in the progenitors of the Lycopodinous series.

2. Having now considered the first means by which greater spore-production might be promoted, viz., by increase in number of sporangia produced in ordinary sequence, and having seen that it has probably been exemplified in *Lycopodium* and *Selaginella*, we may consider the second, viz., *increase in size of the individual sporangium.* This may involve any one or all of the dimensions* of the sporangium; *e.g.*, the sporogenous tissue might be extended (*a*) in a radial direction, as regards the whole strobilus, or (*b*) in a tangential, or (*c*) it might be deepened, while retaining the same area on the sporophyll; or there may be various combinations of (*a*), (*b*), and (*c*).

Within the genera, *Lycopodium* and *Selaginella*, the *depth* (*c*) of the sporogenous mass remains more constant than the other dimensions of the sporangium, and the archesporium is, with the exception of a few abnormal cases, defined by the first periclinal wall. There is apparently a physiological explanation of the fact that the depth of the sporogenous mass is almost uniform; the limit is probably imposed by the difficulty of transmission of nutritive materials upwards from the sub-archesporial pad throughout the developing sporogenous mass: this point will not therefore be considered further at present.

The radial (*a*) and tangential (*b*) dimensions are, however, less constant, and the fluctuations in the genera in question are of importance as leading to a comparison with other forms.

Taking first (*a*), the radial dimension, we see in *Phylloglossum*, and in *L. Selago*, and others, that the sporogenous tissue is referable in the radial section to a single cell, and these species have a comparatively narrow, radially compressed sporangium; in other species, the base of the sporangium is broader, and the sporogenous tissue is referable to *two* (*L. inundatum* and *Selaginella*) or even to three cells (*L. clavatum* and *alpinum*) in each radial section. The fluctuations, which are thus comparatively trifling in *Lycopodium*, acquire a new interest when the sporangia of *Isoetes* and of *Lepidodendron* are compared. In the former, the mature sporangium is rather like an oval cake, with its major axis in the radial direction, the sporangium not being radially compressed as in *Lycopodium.* Obviously here is an increased accommodation for spore-production as compared with *Lycopodium*, brought about by increase of the radial dimension. The development bears this out, for the archesporium is referable to a considerable number of cells in each radial section. Finally, in *Lepidodendron,* this radial extension attains its maximum, the mature sporangia being more than three times as long (radially) as they are broad (tangentially), and the possibility of production of large numbers of spores is thus greatly increased.

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* It is to be noted that the comparison is not based upon absolute measurement, which might be misleading, but rather upon tissue-complexity; one spore-mother-cell, though a small one, will give rise to four spores, which, though small, may yet serve to produce four new individuals, just as well as four large ones.

Turning now to (*b*), the tangential dimensions, considerable fluctuations are to be found in our series. Perhaps the simplest case is that of *L. phlegmaria,* where the sporogenous tissue appears to be referable in tangential section to *two* cells. Passing to *Selaginella spinosa,* it is referable to *three* or *four;* in *L. Selago,* it is referable to about *six;* in *L. clavatum* and *alpinum,* about twelve. These figures, relating as they do to early stages of development, give, nevertheless, a clue to the final form and dimensions of the sporangia: while the sporangium of *Selaginella* is very little extended tangentially, and hardly shows any trace of the kidney-like form, that of *L. clavatum* assumes the form of an inverted U (fig. 92, *c*, *c*). The behaviour of the sub-archesporial pad is also worthy of note, since, in such forms as the last, it attains a very considerable degree of development, and projects far upwards into the cavity of the sporangium.

It is thus seen that the various dimensions of the sporangium are susceptible of fluctuations, in different genera and species, and, as one or more of the dimensions is increased, the individual sporangium may attain, when mature, a very considerably increased size, *e.g.*, those of *Isoetes* and *Lepidodendron.* But when this is the case, the enlarged sac is exposed, both to risks of damage from without and to difficulties from within in the supply of nourishment to the large mass of developing spores. It is, doubtless, these two factors which have led to those peculiar developments known as the trabeculæ of *Isoetes,* and the somewhat similar growths now described for *Lepidodendron.* In neither of these plants do the sporangia appear to be completely partitioned; but bands, or plates of sterile tissue (trabeculæ) spring from the sub-archesporial pad, and pass upwards through the sporogenous tissue, and, at least in *Isoetes,* are continuous to the upper wall of the sporangium, but it has not been possible to prove this continuity in the case of *Lepidodendron.* Small upgrowths of a somewhat similar nature have been found at times in *L. clavatum* and *alpinum.* The physiological importance of these is plain; they probably serve as channels for conveyance of nutritive materials into the very mass of developing spores, and they increase the available surface of such transmission. It is specially interesting to note their presence in those Lycopod-sporangia which are the largest, and most extended in a radial direction.

In *L. clavatum* and *alpinum* (and, perhaps, also in *Lepidodendron*) the trabeculæ appear to be mere upgrowths from the sub-archesporial pad. In *Isoetes,* however, it was shown by GOEBEL, and now amply verified, that they are formed by sterilization of part of a potential archesporium; here they are continuous to the upper wall, and probably serve also a mechanical purpose. It has been suggested that they serve as props of the wall at the time when the sporogenous mass is semi-fluid (FARMER, 'Annals of Botany,' vol. 5, p. 49); they may so act, but the peculiar dimpled appearance, often seen in the upper surface of a microsporangium, would rather suggest that they act as stays, in fact similarly to the trabeculæ of *Caulerpa*, as suggested by JANSE ('Pringsh. Jahrb.,' vol. 21, p. 272), and are, at the critical period, in a state of tension.

In *Isoetes* the trabeculæ are not uncommonly connected either by their branchlets (figs. 112, 113), or laterally along a considerable distance so as to form plates, which may also be connected with the walls. Such appearances suggest an approach to a partitioned state of the sporangium, which, however, has not been found in any of the plants hitherto considered. The advantages of a partitioned condition, where the sporangium is large, are plain enough; not only would the nutritive surface adjoining the developing spore be enlarged, but mechanical strength would be afforded to the large developing sac, and, finally, while a single puncture of the large non-septate sporangium by animal, or other agency, would probably destroy the whole mass of spores, if the sporangium were septate only one compartment would suffer. It is clear then that where the size of sporangia is larger, the advantage of a septate condition will become greater. These considerations, together with the facts drawn from *Isoetes*, suggest the question whether such partitioned sporangia of the Lycopodinous type occur, and, if so, in what plants?

A striking answer to this question is, I believe, to be found in a genus of Lycopodineous affinity, in which the sporangium is extended in the radial direction. We have already noted fluctuations in this dimension within the genus *Lycopodium* (compare figs. 36, 58, 73), while *Isoetes* in which the potential archesporium is partially sterilized to form the trabeculæ, is a still more pronounced example among living plants. As will now be explained at length, it is in *Tmesipteris* that we appear to find a comparatively simple septate sporangium, or synangium—which, on the ground of the above considerations, appears to be a more efficient type of construction than such trabecular sporangia as are seen in *Isoetes* or *Lepidodendron*.

PSILOTACEÆ.

The Psilotaceæ are a family which occupies a place somewhat apart from other Lycopodineæ, though they are usually classed with them; their conformation is in many ways distinct from that of other forms, while the two genera of the family, viz., *Psilotum* and *Tmesipteris*, show fundamental similarity to one another, though sufficiently distinct in details.

It is probably owing to their somewhat separate position, and their marked peculiarities, that they have been the subject of frequent discussion, both from the purely morphological, and also from the systematic point of view. The morphological discussions have chiefly centred round the spore-bearing members (synangia or sporangiophores); it is unnecessary to criticise in detail the views which are, or have been held, for this has already been done most admirably by SOLMS-LAUBACH ('Ann. d. Jard. Bot. d. Buitenzorg,' 4, p. 139, &c.), while a very complete list of literature up to the date of his writing is given, together with brief critical remarks, as an appendix to his memoir (*loc cit.*, p. 187). Since then further observations have been made by M. DANGEARD ('Le Botaniste,' série 2, May, 1891), and by Mr. VAUGHAN JENNINGS ('Proc. Roy. Irish Acad.,' series III., vol. 2, 1891), but their statements do not materially alter the position, or determine the points at issue. It is to be remarked that, notwithstanding all that has been written, the knowledge of the facts of development of the peculiar spore-bearing members is still incomplete; their mature structure has been described and figured with all necessary detail by M. BERTRAND ('Arch. Bot. du Nord,' vol. 1, p. 457, for *Psilotum*, and p. 528 for *Tmesipteris*), and others; the external form of the developing organs has been beautifully illustrated for *Psilotum* by SOLMS-LAUBACH (*loc. cit.*, Plate 23), and by BERTRAND (*loc. cit.*, p. 462, fig. 199); drawings have also been made of the young sporangiophores of *Tmesipteris* by GOEBEL ('Bot. Zeit.,' 1881, Plate 6, fig. 12), and by JENNINGS: but the internal details are very incompletely known, the only accounts hitherto published being those of JURANIYI ('Bot. Zeit.,' 1871), which is not illustrated, and of GOEBEL ('Bot. Zeit.,' 1881, p. 688, Plate 6, figs. 9–12). Thus there is need for the subject to be taken up afresh, and the internal details of development to be described, before the morphological question can be finally decided.

The chief views as to the nature of the sporangiophores are these: (1) that the whole sporangiophore is a single appendicular (foliar) member, (2) that it is a structure of reduced type, consisting of an axis bearing a terminal synangium, and two leaves.

The former view (1) was held by all the older morphologists; it was accepted by METTENIUS ('Bot. Zeit.,' 1867, p. 98), and by LUERSSEN, and has been most ably defended, on the basis of observations of external form during development, by Graf SOLMS (*loc. cit.*). The second view was propounded by JURANIYI ('Bot. Zeit.,' 1871, p. 177), and has been adopted by GOEBEL on the basis of his own observations ('Bot. Zeit.,' 1881, p. 689). The arguments have turned upon the position of the organic apex of the whole lateral structure, and the relations of the other parts to it in point of time and place of their first appearance. Obviously, this may be determined either by external observation or by histological analysis of the developing parts, but best by a combination of both methods.

JURANIYI and GOEBEL state that the synangium is actually terminal on the sporangiophore, and this view is very distinctly stated also by M. BERTRAND ('Arch. Bot. du Nord,' vol. 1, p. 463). Graf SOLMS, however (*loc. cit.*, p. 180, and Plate 23), has also described and illustrated the external characters for *Psilotum*, while, at the same time, he suitably criticises the results of other observers which differ from his own. He finds that the sporangiophore first makes its appearance as a lateral flat extension of the growing point of the shoot, which is soon separated from the latter by a very shallow groove: at this time the young sporangiophore has a tongue-like form, being slightly channelled on the upper surface. In the middle of this slight median channel a flat upgrowth appears, and this is the young synangium, which thus arises, according to SOLMS, from the upper surface of the sporangiophore. On the basis of these observations he maintains the older foliar view of the sporangiophore.

Our purpose will now be to see how far the study of radial sections, traversing the apex of the axis and the very young sporangiophores, will bear out this account of the development. Of the two genera the parts in *Psilotum* are more shortly stalked in the mature state than those of *Tmesipteris*: the leaf-lobes of the latter are larger, while the loculi of the synangium, being only two, and both in the median plane, this plant is clearly the one which will more readily yield results from longitudinal sections. *Psilotum*, on the other hand, having a trilocular synangium, will be difficult to work in longitudinal section, and only one of the three loculi can possibly be cut fairly in its median plane in any one section. Accordingly, as both genera have been studied, the description of the results for *Tmesipteris* will be given first. The observations were chiefly made on material supplied by Mr. VAUGHAN JENNINGS; I have also to acknowledge specimens from Mr. G. M. THOMSON, sent direct from New Zealand, while one fine apical bud was cut by Professor I. BAYLEY BALFOUR from the living plant in the Edinburgh Botanic Garden.

TMESIPTERIS.

The apical cone of the plant is very variable in bulk: in strong young shoots it may be a broad dome (fig. 118), while in weaker specimens, or those in which apical growth is beginning to fail, it may be comparatively narrow. In the large as well as the small specimens a single initial is usually present (*x*, fig. 118), but its segmentation does not appear to be strictly regular, and it is difficult to refer the whole meristem to the activity of one parent cell. This conclusion is borne out by the appearance of the apex as seen from above (fig. 119), when the initial is seen to have the form of a three-sided pyramid, but the tissue around it is not readily to be parcelled out into groups derived from regular segments: secondary initials (cells marked *o*) also occur frequently. It will be noted that these results materially coincide with those obtained by SOLMS for *Psilotum* (*loc. cit.*).

Passing from the actual apex the sides of the cone are covered externally by deep prismatic cells, which are of somewhat irregular origin, depth, and arrangement: when a leaf or sporangiophore is about to be formed certain of these increase in size, and undergo both periclinal and anticlinal divisions so as to form a massive outgrowth (figs. 120–121), the summit of which is occupied, as seen in radial section, by a single larger cell of a wedge-like (fig. 120, 123) or prismatic (fig. 121) form: it is not improbable that the latter passes over to the wedge-like form as the part develops.

A transverse section of the axis passing through such a young leaf does not disclose any marked feature (fig. 122). In these early states I find it impossible to say whether the part in question will be a vegetative leaf or a sporangiophore, and even when older it is still a matter of uncertainty; it is, however, believed that fig. 123 represents a foliage leaf, and is to be so recognized by the narrow form which becomes more pronounced in the older vegetative leaves: those, however, which are to develop as sporangiophores, soon show an increase in thickness, while they grow less in length: an excrescence of the adaxial surface soon becomes apparent (fig. 124), in which the superficial cells are chiefly involved: the lower limit of the tissues resulting from their divisions is shown by a heavy line in figs. 120, 121, 124, and 125, and from a comparison of these it will be plain that, while the essential parts of the synangium are derived from the superficial cells of the young leaf, the subjacent cells also bear a part, forming a sub-archesporial pad (*p.*, fig. 125). The superficial cells at first form a rather regular series (fig. 120), which may be compared with the cells which give rise to the sporangia in *Lycopodium clavatum*, or in *Isoetes:* they undergo more or less regular divisions (fig. 124), which, however, I have been unable to follow in detail: a band of tissue some four or more layers in depth is thus produced. At about this period certain masses of cells assume the characters of a sporogenous tissue (figs. 125, 125 *bis*, shaded cells); but though they can be recognized as such by the character of the cells, it is exceedingly difficult to define the actual limits of these sporogenous masses. The more superficial tissues, as well as the band intervening between the two sporogenous masses remain sterile, the latter developing into the septum, while the former develop into the walls of the synangium: it is specially to be noted that the origin of the tissue of the sterile septum, which separates the sporangia, seems to be similar to that of the sporogenous masses themselves.

I have not been able to decide whether the archesporium is here defined at once by the first periclinal division of the superficial cells (fig. 120), or whether successive additions are made to the sporogenous tissue by subsequent periclinal divisions of superficial cells, as in *Equisetum*, and in a less degree in *Isoetes* and *Selaginella.* I am, however, inclined to think the latter to be the case, since in such examples as that shown in fig. 124, the superficial cells are very deep, while the lower cells are not so.

As the development proceeds, the original arrangement of the cells becomes disturbed by unequal growth (fig. 126); the more superficial layers develop into the rather massive wall, and the cells immediately surrounding the sporogenous masses become compressed, and ultimately disorganized. It has been above noted that it is difficult to recognize with certainty the exact limits of the sporogenous masses in the synangia (compare fig. 126): this is probably due to the fact that there is no very clearly defined tapetum, nor is the whole of the sporogenous mass used up in the actual formation of spores, but a considerable proportion of the cells composing it, acting as a diffused tapetum, become broken down, and disappear in a manner similar to that to be described more in detail in *Psilotum* (p. 549).

Finally, a strand of vascular tissue, of which the origin may be traced in figs. 124, 125, 126, is formed, extending up the sporangiophore; on entering the synangium, it passes up to the base of the septum, and there branches right and left, the two branch-bundles traversing the margins of the septum (compare figs. 146–148).

When mature, the wall of the synangium consists of a superficial layer of deep cells, with thick cell-walls (figs. 146–148), which are similar to those of the wall of the sporangium of *Lepidostrobus Brownii* (fig. 93), and as in that fossil, so in *Tmesipteris*, a band of thinner-walled compressed cells, three to four layers thick, supports the superficial layer internally (fig. 146). These cells have pitted walls, and are not definitely limited internally, but irregular tatters of cell-wall project into the cavity of the synangium, showing thus that there is no clear limit between the wall of the synangium and the tapetum.

The septum shows in the main a structure similar to this inner band of the wall, with which it is continuous; it consists of a firm plate of narrow tabular cells, four to six layers in thickness, with profusely pitted, woody walls. The septum is also coated by the remains of thinner-walled disorganized cells. As already noted, the branches of the vascular bundle which enters the synangium pass right and left up the margin of the septum (fig. 148); these bundles are seen as bands of tracheides (fig. 146) in transverse sections through the lower part of the septum; the bundles are not sharply differentiated from the surrounding tissues, and it appears to consist only of xylem. A number of tracheides, continuous with the bundle, extend along the central part of the septum; and from the position of the bundle, it appears to belong to the septum, rather than the external wall of the synangium. Moreover, it will subsequently be seen that the branch vascular bundles are absent in those abnormal synangia in which the septum is wanting or incomplete.

Turning now to sections in other directions, if a synangium be cut vertically (along a line *x*, *x*, fig. 125), the appearance presented is as in fig. 127; *l*, *l* are the lateral lobes (leaves of some writers), which grow out right and left from the summit of the sporangiophore. The shaded cells are the sporogenous mass, and the arrangement of the walls supports rather than discountenances the view that the archesporium is not defined by the first periclinal division of superficial cells; it is easy to see the correspondence between figs. 127 and 125.

If the sporangiophore be cut through transversely, the appearance at successive ages would be such as is shown in figs. 128–131. When very young the outline of the section will be oval (fig 128), the lateral lobes not having as yet appeared: the cells adjoining the axis may be recognized as those which will form the sporangium. It must be noted that they are necessarily cut obliquely, as reference to fig. 124 will show; hence the superficial cells appear shallower than they really are. When rather older (fig. 129) the formation of the leaf-lobes will have begun (*l*, *l*), which then proceeds rapidly (fig. 130). Meanwhile the sporangium (in these transverse sections it is the lower of the two loculi of the sporangium which is cut through) becomes broadly convex, and the steps of the development, as shown in figs. 130, 131, will be seen to coincide with what has been already stated for the radial section.

The above descriptions are based entirely upon the developmental study of normal specimens of *Tmesipteris;* whatever value readers may be disposed to accord to evidence from examination of abnormalities, it is of importance to see what it amounts to, since such evidence has been repeatedly used by previous writers on the Psilotaceæ, though chiefly with reference to *Psilotum.* The importance of such evidence will vary in different cases, according to the frequency of occurrence of any given abnormality: other things being equal, it appears to me that those abnormalities which recur most frequently in a given species will be those which are most worthy of consideration for morphological argument.

As far as I am able to judge from the specimens in my possession, *Tmesipteris* is an unstable plant as regards form. Twenty-four plants have been examined, and upon these were found twenty-six synangia which showed abnormal development—an average of more than one on each plant: they were, however, unequally distributed, some plants bearing no abnormal synangia, others bearing several. It would thus appear that *Tmesipteris* is unusually prone to variation in details of its synangia.

The abnormalities may be considered first from the point of view of external form: it has been a matter of frequent observation that "double leaves" occur in *Psilotum* without a synangium: SOLMS remarks, however (*loc. cit.*, p. 175), that the rudiment of a synangium may almost always be detected in such cases in the usual position. An example of this is shown in fig. 149, for *Tmesipteris,* where the abortive synangium (*sy.*) is seen in the normal position: it is to be noted that it is placed on the adaxial face, and below the indentation between the leaf-lobes. This is then a simple case of arrest of the whole synangium. Similar specimens of *Tmesipteris* have been figured and described by M. BERTRAND ('Arch. Bot. d. Nord,' vol. 1, p. 475). Either the upper or the lower lobe of the synangium may be arrested, while the other lobe develops in the usual way; these two cases are shown in figs. 150, 151; such examples of arrest of development of one loculus are to be carefully distinguished from cases to be described below, showing, in various degrees, the disappearance of the septum between the loculi. A correlative vegetative growth, following arrest of the synangium, was rarely found: in fig. 152, however, a long process is seen bearing two small lobes; this arises in place of the synangium, and is clearly seated, as before, on the adaxial face of the sporangiophore. A different form of correlative growth is seen in fig. 153: a "double-leaf" of abnormal form is here shown, in which the lower part has virtually the form of the single foliage leaf: seated on the adaxial face, and near its base, is a small brown process, which resembles an abortive synangium (*sy.*), while the upper part assumes the character of the "double-leaf," but with the lobes partially coherent. I have not seen in *Tmesipteris* any case of appearance of a third lobe, as described by SOLMS for *Psilotum* (*loc. cit.*, p. 175, Plate 23, fig. 8). In the abnormalities thus described, I see nothing inconsistent with the hypothesis above put forward: that described last (fig. 153) appears decidedly to support the suggestion, based on study of the normal development, that the sporangiophore is a single leaf with two lobes, bearing the synangium on its adaxial face.

It is well known that both *Psilotum* and *Tmesipteris* show alternating sterile and fertile portions of the same shoot, similar to those seen in *Lycopodium Selago*, and other species. It is at the upper or lower limits of these fertile zones that abnormalities are most frequent, and even sporangiophores, which are otherwise normal, show there great variations in vegetative development; thus, fig. 154 represents a sporangiophore from the middle of a fertile zone, with fully developed leaf-lobes, while fig. 155 represents one of similar age from the upper limit of the fertile zone; here the leaf-lobes are small and stunted, though the synangium shows its normal characters. The synangium itself is, however, liable to variations in form of a somewhat parallel nature, involving (i.) greater complexity, or (ii.) simplification as compared with the normal. In two specimens from the middle of the fertile zone, a trilocular synangium was seen (fig. 156), the position of the three loculi being similar to those in *Psilotum*, with which the correspondence of the whole sporangiophore is in these exceptional cases very close. Fig. 157 represents a less regular case where three loculi are seated on one sporangiophore.

But the greatest interest in connection with the hypothesis above put forward is centred in those abnormal synangia which show *simplification* of external form, and it will presently be shown that simplification of internal structure follows that of form: such simpler synangia are most frequently, though not exclusively, found at the limits of the fertile zone, or on specimens which have developed weakly. The most frequent simplification is found in the absence of the groove separating the two lobes of the synangium, so that externally the synangium appears as a single boat-shaped body (fig. 158). In others the form may be shorter (fig. 159), but in such specimens, of which the internal structure will be seen to present facts of the greatest importance for our theory, it is to be noted that the two projecting points, as well as the slight median groove, show that the whole body represents a complete synangium of a reduced type; it is not to be ascribed to the arrest of one or other of the loculi, as in figs. 150 or 151. Finally, in fig. 160, we see an extreme case of reduction, the synangium being here represented by a small spherical body, borne in the usual position on a sporangiophore, of which the leaf-lobes are of a very small size. The above examples will show the chief lines of modification of form to which the synangia are liable; but the more direct interest in connection with our hypothesis is to be found in the modifications of internal structure and development which accompany them.

The normal structure of the synangium and its development have been described in detail above (p. 541–543); examination of sections of such synangia as those we have just been discussing shows considerable deviations from the normal structure, especially as regards the partial or even complete abortion of the septum; these deviations have a certain relation to the external form. The structural details to be now described have been obtained by the comparison of sections of fourteen specimens of different ages. Those of the type shown in fig. 158 deviate the least from the normal in form, and in section these sometimes show a complete septum, of apparently normal structure; of the others, however, which were approaching maturity, one showed only a slight flange, projecting inwards into the single large cavity; this doubtless represents the margin of the septum, of which the central part has disappeared, *in other specimens there was no representative of the septum at all.* From the form of these synangia, as well as from the occasional presence of vestiges of the septum, we learn that they are not due to abortion of one-half of the synangium, but that they represent the whole synangium, and they thus demonstrate *that the septum may be partially or completely abortive.* The same was found to be the case in the specimen shown in fig. 160, but the best results have been obtained from those of the type shown in fig. 159, for several of these of different ages were obtained, sufficient indeed to supply the most essential features in the development of these non-septate synangia. It has already been shown in the development of normal synangia, that it is impossible in early stages to differentiate the sporogenous tissue from the septum, and that in later phases the limit was not clearly marked (see p. 542); in the non-septate synangia the distinction never appears, or, at most, it is only slightly suggested. Such a synangium in the young state is shown in fig. 161, from which it will be seen that the form of the synangium is of the type of fig. 150, the groove between the lobes being almost obsolete; the vascular bundle stops short at the base of the synangium, instead of passing far into it, as described for the normal type; the place where the septum should be is indicated by a slight flange of firmer tissue projecting downwards from the upper wall (figs. 161, 162), but instead of continuing downwards as firm tissue, as in the normal synangia, it merges into a mass of cells which fill the synangium, and consists of (i.) cells with less dense contents (the tapetum, *t*, fig. 162), and (ii.) more densely protoplasmic cells (the sporogenous cells, *s*, fig. 162); the former appear as a peripheral band (*t*, *t*), while the latter (*s*, *s*) occupy the centre. The place where the septum should be demands special notice: there the tissue is disposed, roughly speaking, in rows, as in the normal synangium; the tissue opposite the projecting flange of the incomplete septum appears to be sometimes of the tapetal character, and disappears as the synangium develops (fig. 163). *But its cells may also be sporogenous* (fig. 162); in the younger state they may be so recognized by their denser protoplasmic contents, as in the figure above quoted, but the best demonstration of this fact is afforded by later stages, where the sporogenous cells are more clearly distinguished, by their definite cell-walls and nuclei, from the tapetal cells which are undergoing disorganization. Fig. 164 shows a whole synangium of the same type as fig. 159, cut in median section; there is hardly any groove defining the two halves of the synangium, and no clear indication of the septum internally, while the cavity is occupied partly by disorganized cells of the peripheral and diffused tapetum, partly by the sporogenous cells, which hang together in connected masses. In fig. 165 part of the contents of this synangium, lying about the centre of it, are represented under a high power, while the line (x, x) shows the position which the septum should normally occupy at present. Now it is plain that a connected thread of sporogenous cells, with definite cell-walls and nuclei, which make them readily distinguishable from the tapetal cells, extends quite across that line; thus it is demonstrated that *the tissue which would normally develop as the septum, may, on occasions, develop as tapetum, or even as sporogenous tissue.*

Figs. 166–168 illustrate other examples of a similar nature, which were also of size far below the normal. Figs. 166, 167 show two transverse sections of a small synangium, the first near its base, the second nearer to its upper surface. From these it will be seen that a *partial septum* was present (*s.*), which projects from the upper wall of the synangium for a certain distance downwards into the cavity, but there stops short. Finally, fig. 168 represents a transverse section through the small spherical synangium shown in fig. 160, and in it no trace of a septum was found, the single cavity being occupied by immature spores (*sp.*).

The modification of the vascular system of the synangium where the septum is absent is worthy of mention. It has already been stated that in normal synangia a vascular bundle enters the stalk, and that strands, consisting chiefly of tracheides, branch right and left, entering the septum, and running along its margin about four layers of cells from the outer surface. In synangia, where the septum is incomplete or absent, I find no such septal bundles; in these cases the vascular supply seems to stop short at the base. This behaviour of the septal bundles shows an obvious correlation with the complexity of structure of the whole synangium.

The details described in the above paragraphs occur in synangia, which will commonly be designated "abnormal." In so far as they differ from the common type, they are rightly so called; but it is to be remarked that there is some method in their abnormality; their occurrence, especially at the limits of the fertile zones, the frequency of their appearance, and the correlation of smaller size and greater simplicity of external form of the synangium with the imperfect development, or even entire absence of the septum, all point to the conclusion that this is not a case of haphazard monstrosity. The whole series appears to me to illustrate within the one species what has been recognized elsewhere for distinct genera, such as *Lycopodium*, *Isoetes*, and *Lepidodendron*. *Where the sporangium is large, sterile bands of tissue are present, while in smaller sporangia homologous with these, sterile bands of tissue may be entirely absent. But whereas in the other cases quoted the sterile tissue was represented only by incomplete trabeculæ, in* Tmesipteris *the same rule is found to apply to the complete septum.*

It may doubtless be objected that these smaller synangia with simpler structure illustrate the possibility of *fusion* of sporangia normally distinct, rather than that they have any bearing on the question of formation of septa; in fact, that they are extreme cases of a *progressive reduction* in a plant which is on the down grade of morphological change, such as has been suggested by STRASBURGER ('Bot. Zeit.,' 1873), and not cases of individual retrogression in a plant which is, as I should suppose, on the up-grade. But when we look at the whole question from the point of view of increase of number of spores, and compare *Tmesipteris, Lepidodendron,* and *Lycopodium,* if the line of advance were such as I suggest, it is just at the limits of the fertile zone that individual retrogression to simpler types would be expected, and the physiological explanation of their occurrence would be the running short of nutritive supply, from which would follow the development of synangia of smaller size and less complex structure.

The results from the study of the development in *Tmesipteris* may be summarized as follows :—

1. In their earliest stages the foliage leaves are not readily distinguishable from the sporangiophores either in form or in internal structure, and they occupy a similar position to them upon the axis.
2. In either case a prismatic or wedge-shaped cell occupies the apex, as seen in radial section, but all the tissues are not readily referable to the segmentation of a single cell.
3. The first appearance of the synangium is as an upgrowth of superficial cells of the adaxial face, immediately below the apex of the sporangiophore; cells of the abaxial side also grow strongly, while the apex itself does not grow; so that the organic apex is soon sunk in the groove between these stronger growths.
4. The superficial cells of the adaxial surface, which are to form the synangium, undergo periclinal and anticlinal divisions, so as to form about four layers; from these are differentiated : (*a*) two sporogenous masses, (*b*) a septum between them, (*c*) the superficial wall.
5. The limits of the sporogenous masses are difficult to define ; this is owing to the fact that there is no definite tapetum, while many of the cells of the sporogenous tissue also become disorganized without undergoing the tetrad division.
6. The tissue of the septum is similar, as regards origin, to the sporogenous masses ; it is therefore possible to regard it as a sterilized portion of a potential archesporium.
7. The lateral leaf-lobes begin to be formed almost simultaneously with the synangium.
8. In synangia of abnormally simple form the septum may be partially or completely abortive.
9. The tissue which normally develops as the septum, may on occasions develop as tapetum, or even as sporogenous tissue.

PSILOTUM.

JURANYI ('Bot. Zeit.,' 1871, p. 177) appears to have been the first to investigate the internal details of development of the sporangiophore in *Psilotum;* he describes it, when young, as having all the characters of an axial papilla, noting the presence of a cambial strand, which he stated to be absent from the foliage leaf. In this, however, he was mistaken according to SOLMS (*loc. cit.*, p. 184). He admits the close similarity of the sterile and fertile parts while young, as regards their external form, a point which has above been specially noted for *Tmesipteris.* He describes the synangium as occupying the apex of the lateral appendage or sporangiophore, while a three-sided pyramidal initial cell is present with definite segmentation. STRASBURGER denies the last facts ('Bot. Zeit.,' 1873, p. 92), and GOEBEL agrees that an initial cell is not present. He maintains, however, that the synangium is of terminal origin on the sporangiophore, and describes the sporogenous tissue of each loculus as referable to a single archesporial cell, but this single cell he has not observed ('Bot. Zeit.,' 1881, p. 692). The tapetum appears to originate from the sporogenous tissue. The above are the chief results obtained by previous investigators on the internal details of early development in *Psilotum.*

The detailed study of the synangium of *Psilotum* by means of sections is more difficult than that of *Tmesipteris* on account of its tri-locular character. In radial sections through the terminal bud, the young sporangiophores are found to present a general outline and structure similar to those of *Tmesipteris* (compare figs. 134, 136). Fig. 134 shows one such: the cell (×) is believed to represent the organic apex of the sporangiophore, though it is doubtful whether it be this initial which gives rise to the whole mass of the tissue. The synangium thus appears as an outgrowth of the upper surface of the sporangiophore, while the tissue on the abaxial side of it is already growing out into a bulky projection, as has been noted by GOEBEL (*loc. cit.*, p. 693), and as already seen in *Tmesipteris.* But I have not been able to trace the development of the essential parts of the loculi of the synangium from the superficial cells of the adaxial side of the sporangiophore in this case with the same certainty as in *Tmesipteris:* I think this is chiefly owing to the stalk being here narrower, and to the fact that only one loculus of the synangium can be cut in a median direction in any one section; supposing this to be the median plane of the whole sporangiophore, then it will be the abaxial loculus which will be thus traversed. And here it may be noted that GOEBEL'S fig. 11 (*loc. cit.*) does not appear to traverse either of the two loculi exactly in a radial plane; if this were so, the two loculi could not appear so nearly equal in size, and accordingly as both are traversed more or less obliquely the results from the section must be accepted with reservation. A truly radial section of a young synangium is shown in fig. 135, the arrow indicating the direction of the main axis; the cell (×) in figs. 135, 137, is a conical cell, which is commonly, though perhaps not constantly found occupying the centre of the apical surface of the synangium (compare figs. 136, 139, 141). Divergent statements of other writers have been above noted as relating to the presence or absence of an initial cell in the synangium of *Psilotum.* JURANYI ('Bot. Zeit.,' 1871, p. 179), describes the synangium as growing with an initial cell of the form of a three-sided pyramid. STRASBURGER ('Bot. Zeit.,' 1873, No. 6), and GOEBEL ('Bot. Zeit.,' 1881, p. 692, and fig. 9, *sp.*) deny that there is one. I can confidently state that a small three-sided pyramidal cell is commonly present in my preparations (× figs. 135, 137), though I am not disposed to assert that this is the primary parent cell of the whole synangium. The cell shaded in fig. 135 is believed to be the archesporial cell for one of the loculi, but after comparison of a large number of sections I am still uncertain whether the whole of the sporogenous tissue in each loculus is really referable to a single parent cell, for just the same difficulty arises here as in *Tmesipteris*, in recognizing the exact limits of the sporogenous masses; here again, this is probably due to the facts (1) that there is no clearly defined tapetum, and (2) that only a part of the sporogenous tissue actually forms spores. The Psilotaceæ are in this respect the most difficult family of the Vascular Cryptogams.

The subsequent stages of development are illustrated by figs. 136–138, and it will be seen from these how the sporogenous masses assume large dimensions, and are at first composed of uniform cells. The wall of the synangium meanwhile becomes multiseriate, and the cells of the outermost layer assume a deep and prismatic form, while the inner layers are narrow. The same is the character of the more superficial cells of the sporogenous mass (fig. 138), so that it is almost impossible to recognize the limit between the tissue of the wall and of the sporogenous mass; the superficial portions of the latter become disorganized without the formation of spores, but there is no clearly defined tapetum. Such is also the fate of a considerable proportion of the more central cells. As the synangium develops, irregular groups of cells of the sporogenous masses assume dense granular contents, and subdivide, while the others remain paler, with more watery contents, and do not divide; the former undergo the final tetrad division, and form spores, while the latter become disorganized. The actual state of partial disorganization is shown in figs. 143, 144; thus, a partial sterilization of cells of a sporogenous tissue, essentially similar to that demonstrated in *Equisetum*, is seen also in *Psilotum*, and, as above stated, it exists also in *Tmesipteris*. This has already been noted by STRASBURGER.

The fan-like tracery of the cells, as seen in radial section of the synangium, shows that the study of transverse sections will present difficulties; these are least in the youngest stages, such as that shown in fig. 139, which corresponds in age nearly to that of fig. 135. The cells shaded are believed to be the archesporia, but I should be slow to make precise statements on this point, and especially so in face of the difficulty, above noted, of assigning definite limits to the sporogenous tissue in older synangia. Further stages of development are shown in figs. 140–142; and when allowance is made for the transverse sections cutting the cell-rows rather obliquely (as must be the case in parts with a fan-like tracery), it will be seen that the transverse sections fit with all reasonable closeness of comparison with the results from the longitudinal.

The main facts derived from the study of *Psilotum* thus coincide with those arrived at in *Tmesipteris*, as regards the origin of the sporangiophore, and the appearance of the synangium on its upper surface, below the extreme apex. The following points may be noted as more specially applicable to *Psilotum*, in addition to those already summarized for *Tmesipteris* :—

1. The organic apex of the sporangiophore coincides with the groove between the synangium and the pair of abaxial growths (leaf-lobes), as seen in the mature state.
2. A three-sided pyramidal cell is usually present at the apex of the synangium.
3. Each sporogenous mass appears to be referable in origin to a single parent cell, but this has not been actually proved, it being difficult to assign sharp limits to the sporogenous masses.
4. The inner cells of the wall, as well as the superficial cells of the sporogenous masses, become disorganized, but there is no definitely distinguished tapetum.
5. Certain cells of the sporogenous tissue scattered through the mass, are destroyed without forming spores, as is also the case in *Equisetum* and in *Tmesipteris*.

THEORETICAL TREATMENT OF RESULTS FROM PSILOTACEÆ.

The observations above detailed show that the study of development by means of sections supports the observations of SOLMS, rather than those of JURANIYI, GOEBEL, and BERTRAND. We conclude from examination of sections, very clearly in the case of *Tmesipteris*, though with less clear demonstration in the more complex case of *Psilotum*, that the synangium is a product of the adaxial surface of the sporangiophore, and that it arises immediately below the organic apex of that part. These facts strengthen the conclusion already drawn by SOLMS from external observation, that the whole sporangiophore is a member of foliar nature, and that it is not composed of a shortened axis and leaves, as JURANIYI suggested. I would add that, even if the synangium had proved to be terminal, there would be no need to have recourse to so cumbrous, and I think improbable, an explanation of the fact, for to me it seems just as probable that a synangium may occupy the apex of a leaf, as that a sporangium may be found at the apex of an axis; in this case the terminal or lateral position of the synangium would not affect the argument. This seems to have been the view of PRANTL also.

The lateral position of the synangium being demonstrated, and the conclusion arrived at that the whole sporangiophore is a foliar structure, it remains to draw comparisons with other plants, and in the first place with those to which the affinity of the Psilotaceæ has always been recognized, viz., the Lycopodiaceæ. The comparison will first relate to *Tmesipteris*, which is probably nearer akin to *Lycopodium* than is *Psilotum*. If figs. 120, 121, 124 of *Tmesipteris* be compared with fig. 58 of *L. clavatum*, or better with figs. 71–74 of *L. alpinum*, the similarity will be obvious; in both cases an outgrowth has appeared on the upper surface of a leaf, involving a number of cells, which are undergoing anticlinal and periclinal divisions; but whereas the growth in

Lycopodium is close to the base of the sporophyll, that in *Tmesipteris* is strongest close to the apex; this is the most salient point of difference at this stage. It may, however, be noted that an intermediate condition is seen in *Isoetes* (compare figs. 105, 106, 107), where the sporangium is seated slightly above the basal limit of the sporophyll; also in *Lepidostrobus,* where also there is an interval between the lower limit of the sporangium and the insertion of the sporophyll on the axis; also that there is some variety in the relation of the sporangium to the sporophyll in *Selaginella* and *Lycopodium.*

The tangential section of the sporangium in certain species of *Lycopodium* shows a very considerable curved series of archesporial cells (figs. 42, 64, 76); in *Tmesipteris,* the cells so exposed appear to be only two (figs. 127, 129, 130); this difference is, however, not very material, for we find somewhat similar variation within the genera *Lycopodium* and *Selaginella.* Thus, while the number of archesporial cells seen in tangential section in *L. clavatum* is large, in *L. phlegmaria* (fig. 50) it is at most four, or perhaps even two; accordingly, this difference is one of only secondary importance. Some of the various ways in which the dimensions of Lycopodinous sporangia may vary have been discussed above (p. 536, &c.); it has been shown that there is variety within the genus *Lycopodium* in the number of archesporial cells as seen in the radial section, *L. Selago* showing the simplest type, with only one archesporial cell thus seen (fig. 36), while *L. clavatum* will serve as a more complex type with three (fig. 58). It has been pointed out (p. 532) that in *Isoetes* the number of archesporial cells exposed in the radial section is larger (figs. 105, 106), while the existence of this more extensive sheet of archesporial tissue is accompanied by the formation of trabeculæ, which are, as regards their origin, sterilized portions of a potential sporogenous tissue. It has also been above suggested that the large oblong sporangium of *Lepidostrobus* owes its origin to a similar extensive development of the sporogenous tissue, which probably stretched in a radial direction for a considerable distance along the upper surface of the sporophyll (fig. 94); though not septate, the cavity of the sporangium is traversed by trabeculæ (figs. 96–103), or even irregular continuous plates (figs. 132, 133) of sterile tissue; at present, unfortunately, no developmental data are available for proving whether or not these sterile tissues were derived from a potential archesporium, but their great similarity to the sterile trabeculæ of *Isoetes* makes it probable that they were.

Like *Lycopodium* and *Isoetes, Tmesipteris* shows also an extensive potential archesporium, but here it occupies a narrow zone on the upper surface of the sporangiophore, and extends for a considerable distance in a radial direction, stretching to its extreme apex. It is not, however, fertile throughout in normal synangia, for while the portions at either end develop so as to supply the contents of the two large loculi, the middle portion is sterile and develops normally as the septum. Thus, on developmental grounds, it appears that the synangium of *Tmesipteris* corresponds in position to the sporangium of *Isoetes* or *Lepidostrobus,* being produced on the upper surface of the sporophyll or sporangiophore, but at some little distance from the base, and differing in this respect only in a minor degree from other Lycopods; this points towards the homology of the sporangium of the Lycopods and the synangium of *Tmesipteris*, that is, the homology of a single sporangium with a synangium bearing two loculi—a non-septate with a septate body. Clearly, before such a conclusion could be admitted, it will be necessary to examine the evidence very closely.

There are three lines of evidence—(i) from comparative anatomy of the plants in question; (ii) from comparative study of normal development and mature structure of their spore-bearing organs; (iii) from study of abnormalities.

(i) I have already shown elsewhere ('Annals of Botany,' vol. 7, p. 329) that the vascular tissues of *Lepidostrobus Brownii* show an extraordinary similarity to the corresponding tissues of the *Psilotaceæ;* it may be stated that this correspondence is closer than with any other living plants, closer even than with *Lycopodium.* The affinity of *Lepidodendron* has always been recognized with the Lycopods; we now see that, as regards the vascular system, it is more especially with that outlying group of Lycopodineæ, viz., the Psilotaceæ.

(ii) The evidence under our second head in support of the homology has been dealt with at length in the preceding pages, and need only be again summarized here as follows:—(*a*) the position of the synangium of *Tmesipteris,* and its origin from the upper surface of the sporangiophore (sporophyll), is similar to that of *Lepidostrobus* or *Isoetes;* (*b*) in the general form of the synangium and in the structure of the wall, the synangium of *Tmesipteris* resembles the sporangium of *Lepidostrobus Brownii* (compare (figs. 93 and 146); (*c*) the function of the two parts is the same; (*d*) in *Isoetes,* and also in *Lepidostrobus,* sterile trabeculæ, or plates of tissue, run up into the sporogenous cavity corresponding in this respect, though not in detail of outline, to the septum of *Tmesipteris;* (*e*) the origin of the tissue of the septum in relation to the sporogenous tissue is similar in *Tmesipteris* to the origin of the trabeculæ in *Isoetes.* Its origin in *Lepidostrobus* has not been observed, but there is reason to believe that there was similarity in this respect between these two plants.

(iii) The most interesting evidence is that derived from abnormal synangia of *Tmesipteris,* which show that (*a*) where the form is simpler, and resembles more closely that of the sporangium of *Lepidostrobus, the septum may be partially or completely abortive, and the synangium be thus replaced by a simple sporangium;* (*b*) it has been demonstrated that in such cases *the tissue which would normally form the septum may develop as tapetum, or even as sporogenous tissue.* It is thus seen that there is no essential difference between the tissue which may be formative of septum, and that which may be sporogenous, since the one can pass on occasions into the other. It will be noted that this observation is the converse of what Professor GOEBEL has demonstrated in *Isoetes;* he there showed that *part of a potential archesporium may be sterilized, and develop as trabeculæ.* I have now shown the converse, viz., that *tissue, which, though similar in origin to the sporogenous tissue, usually forms a* *septum, may on occasions form spores.* The conclusion is that, in dealing with such cases, the presence or absence of trabeculæ or a septum is a phenomenon of secondary moment from the point of view of homology, and, in fact, *there is no essential obstacle to recognizing homologies, between parts of which one may be partially or completely septate, the other non-septate.*[*]

From the facts and the reasoning thus briefly stated, I conclude that *the synangium of Tmesipteris is homologous with the sporangium of other Lycopodineæ*, the nearest correspondence being with *Lepidostrobus* and *Isoetes.* It may be looked upon as an amendment on the type of sporangium in these plants; their trabeculæ, though irregular, doubtless yielded physiological, and possibly also mechanical, support. A comparatively slight rearrangement and consolidation of the trabecular tissue of *Isoetes* or of *Lepidostrobus* might result in the complete partition of the sporangium into two loculi, as it is seen normally in *Tmesipteris;* or the converse view is possible, viz., that the imperfectly septate sporangia of the type shown in *Lepidostrobus* or *Isoetes* may have resulted from reduction of completely septate types. This question will be discussed later. At present it may be stated that the former view seems the more probable.

The case of *Psilotum* appears at first sight more difficult; there can, however, be no doubt that the synangium of *Psilotum* is homologous with that of *Tmesipteris*—the similarity of position and structure, and the occurrence of trilocular synangia in *Tmesipteris* (fig. 156), are sufficient evidence of this. Other observers have noted variations from the normal trilocular synangium in *Psilotum.* A reduction of loculi to two is not uncommon, though it appears to be frequently the result of mere arrest of one of the loculi. In other cases the number of loculi may be increased to four or five (SOLMS, *loc. cit.*, p. 174). From such observations it follows that *the number of loculi need not affect our view of homology;* whether the number of loculi be one (fig. 160), two (fig. 154), three (fig. 156), or four, or five, the synangium of the Psilotaceæ is still homologous throughout, while, as above concluded, it is also homologous with the sporangium of other Lycopodineæ.

The presence of the two leaf-lobes, in the fertile leaves of these two genera, is doubtless one of their most peculiar features, as well as most difficult to harmonize with the condition of the leaf in allied plants. The Lycopodineæ are so strongly characterized by the simple form of their leaves, that these parts of the Psilotaceæ call for special attention. It has been repeatedly remarked that the leaves of *Psilotum* and *Tmesipteris* may appear double, though no synangium may be attached, but these cases probably arise by abortion of a potential synangium, and are not to be looked upon as double leaves normally produced; in fact the vegetative leaf in these plants is normally simple, while the fertile sporangiophore bears lateral lobes;

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[*] A somewhat similar case is to be found in the genus *Najas*, in which the single anther may be quadrilocular in *N. major*, but only unilocular in *N. minor*. EICHLER, 'Blüthendiagramme,' p. 82.

these facts must be accepted as they stand, though the Lycopodinous leaf is elsewhere simple, and though it is decidedly exceptional to find sporophylls more elaborate in form than foliage leaves of the same plant. It must not be forgotten that the origin of the sporangiophore is like that of the foliage leaf, and that in *Tmesipteris* the distinction can only be drawn when the development has proceeded to a considerable extent, while the lateral lobes make their appearance *later* than the synangium in both genera, and the synangium appears below the apex of the sporangiophore. These are the facts on which the foliar view is based, notwithstanding the peculiarity of the lobed leaf when mature.

But, though peculiar, the lobes of the fertile leaves may be seen to serve a useful end; here, as elsewhere, the protection of the young synangia is a matter of importance; it is obvious that two lateral leaf-lobes would offer more protection than a single terminal growth of similar form and size; the result is shown for *Psilotum,* in figs. 139, 140, and for *Tmesipteris,* in fig. 145, where the synangium is closely invested by the protecting lobes. Moreover, it is to be remarked that in such cases as these, where the synangia appear as very considerable and bulky bodies on the adaxial face of the leaf, the foliage leaf itself being also flattened in a median plane, the presence of an extended leaf-apex would be highly inconvenient in the packing of the parts in the bud, for the result would be a lax bud, in which the individual parts would be greatly exposed. By the arrest of the apex of the leaf, and substitution of the lateral lobes, as implied in the hypothesis above put forward, a more compact bud is produced, and the synangia are better protected. The arrest of the apex of the leaf may, perhaps, be compared with a similar arrest in the flower of certain Angiosperms, where mechanical inconvenience has led to abortion of stamens or carpels.

On the ground of the above facts and considerations, I conclude that the shoot of the Psilotaceæ (apart from branching in the ordinary sense of the word, which is much more common in *Psilotum* than in *Tmesipteris*) is a simple shoot, consisting of an axis, bearing sporangiophores and foliage leaves. These alternate with one another in irregular zones, and in *Tmesipteris* the transition from foliage leaves to sporangiophores may be frequently repeated, in *Psilotum* the repetition is less frequent. The condition is thus similar to that in *Lycopodium Selago* with its successive sterile and fertile zones. The abortive synangia correspond to the abortive sporangia in this and other species of *Lycopodium,* and accordingly the general considerations as regards origin from a simple strobilus, which were laid down, on p. 535, for the genus *Lycopodium,* will apply with equal force to *Psilotum* or *Tmesipteris.*

CONCLUDING REMARKS.

In the above pages I have described the results of an examination of the spore-producing members of the strobiloid Vascular Cryptogams, viz., Equisetineæ, and

Lycopodineæ, including *Lepidodendron, Isoetes,* and the Psilotaceæ. It may here be remarked that the prime object which I have kept before me has not been directly to trace "homologies" between the parts of various Vascular Cryptogams. It is quite an open question whether true phylogenetic homologies are really to be found between parts of plants which are so distant from one another systematically as, for instance, *Equisetum* and *Lycopodium;* but when plants appear to belong to the same natural series, as, for instance, *Lycopodium, Selaginella, Lepidodendron, Isoetes, Tmesipteris,* and *Psilotum,* then I think that homologies may fairly be traced between their parts. This has not, however, been the first object: the chief end in view has been to disclose some main features of the manner in which the advance from some Algal-Bryophytic ancestry to the Vascular Cryptogams may have been brought about. On earlier pages (p. 485) this question has been first approached by comparative study of the Bryophyta, especially the Hepaticæ. The conclusions arrived at by LEITGEB, the greatest specialist on the minute study of the Hepaticæ, as to the probable mode of progression from the simpler to the more complex types of these plants, suggested the idea that traces of somewhat similar lines of advance might be found among living Vascular Cryptogams; and that these might throw some light upon the question of transition from the Bryophytes to the more complex vascular plants. Four questions relating to this subject were put forward (p. 494), and we shall now see how far answers may be found to them from the observations and comparisons above described.

(1.) Are sterile cells distributed among the sporogenous cells in any Vascular Cryptogams?

In answer to this we find sterile cells in large numbers distributed through the sporogenous masses in *Equisetum, Tmesipteris,* and *Psilotum.* The criticism may be advanced that this is merely a physiological phenomenon depending on nutrition; but in this I see no real objection, for such physiological phenomena have largely affected the course of evolution, and, in fact, morphology should be looked upon as little more than the study of stereotyped physiology. In view of the facts ascertained from the Hepaticæ, we cannot pass over the existence of these sterile cells as a matter of no morphological importance. It is true they do not form firm walls, or develop into cells such as the elaters: they are to be compared rather with the sterile cells in the sporogonium of *Oxymitra* (LEITGEB, *loc. cit.,* Heft 4, p. 43). But whatever comparisons be drawn, the fact remains that sterile cells in large numbers are present in the sporangia of the plants above named.*

(2.) Do any Vascular Cryptogams show distinct parts which may be correlated in position, structure, development, and function with the sporogonial head of Bryophyta?

The strobilus of *Equisetum* is in function the counterpart of the sporogonial head: its normally terminal position is also similar, though the shoot on which it is borne is more complex in structure and in branching. In early stages of development it is not unlike certain sporogonial heads, but as development proceeds it becomes much more complex, showing first outgrowing sporangiophores, and subsequently separate sporangia. While still young, it is possible to recognize superficial cells which will give rise to the essential parts of the sporangia, at a time when the sporangiophores are only slightly projecting beyond the general surface of the strobilus. Like most sporogonial heads it is usually sharply limited below, and rarely shows the power of branching. Similarly, with *Phylloglossum*, the strobilus holds a position comparable to the sporogonial head, though more complex in structure. Its apical growth, while young, is not unlike that of some sporogonia. In most cases it is sharply limited below, and is rarely branched. But in *Lycopodium* and *Selaginella* the strobilus is not so limited, and, as above explained, there is good reason to believe that the chief vegetative region of these plants is the result of sterilization of the lower parts of an extended and branched strobilus. Such development would attain its highest complexity in the tree-like trunks and branches of *Lepidodendron*, of which the cone (*Lepidostrobus*) would still represent the fertile portion of the sporogonial head. In the *Psilotaceæ* the strobili are more lax: as above pointed out, however, on the grounds of development and histology, as well as general comparison of form, we conclude that the case is similar to that of the *Selago* type of *Lycopodium*. Lastly, *Isoetes* may be regarded as a simple strobilus of which certain sterile leaves intervene between the fertile ones. In fact, all the strobiloid types hitherto examined, will fall in, without undue straining of the idea, with the working hypothesis, that the strobilus is the counterpart of a sporogonial head: in function and position the correspondence is usually plain enough: the structure, external form, and details of development are, however, decidedly more complex in the vascular plants, and the correspondence is apparently less close in proportion as the appendicular organs are of relatively larger size.

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* Similar sterile cells are also found in *Ophioglossum.*

(3.) Are the sporangia borne in such relation to one another as to suggest a common origin by subdivision of simpler parts?

In *Phylloglossum*, *Lycopodium*, *Selaginella*, *Lepidostrobus*, and *Isoetes* the sporangia are isolated, a single sporangium being borne on each sporophyll; in these genera there is in the arrangement of the sporangia no obvious suggestion of their having been the result of subdivision of simpler parts. But in *Equisetum* and in the Psilotaceæ the case is different. Each sporangiophore of *Equisetum* bears a number of sporangia; in the young state these appear sunk in the margin of the slightly protuberant sporangiophore; but when mature they project as apparently more distinct parts. The younger state may be taken as an indication of the probable mode of origin by descent, in which case the view would be arrived at that the sporangia of each sporangiophore were originally more closely associated together, and it will not appear improbable that they may have had a common origin, the tissue now intervening between them having been completely sterilized. But before such a suggestion can be seriously considered exact evidence should be forthcoming that sterilization can take place; this will be found in the answer to question (4). In the Psilotaceæ the sporangia are grouped in synangia, the number of loculi varying from one to five; their appearance and arrangement certainly would suggest the idea of a common origin, by subdivision of simpler parts. The similarity of the synangium of *Psilotum* to the sporangiophore of *Equisetum* would indicate that the mode of origin of these parts was probably somewhat similar.

(4.) Is there direct evidence in any Vascular Cryptogam of conversion of potential sporogenous tissue into masses of sterile tissue, or conversely of conversion of sterile septa into spore-producing cells?

Professor GOEBEL has shown that the trabeculæ of *Isoetes* are derived from a potential archesporium; this I can endorse, and it would, therefore, appear that the trabeculæ are parts of a potential sporogenous tissue converted into sterile tissue; the same appears to be not improbable for *Lepidostrobus*.* GOEBEL remarks ('Annals of Botany,' 1892, p. 358) that he "would only attach a biological, that is, an adaptive, significance to the fact." My point is that the requirements so well met by *Isoetes* in the formation of its sterile trabeculæ, probably made themselves felt in other plants with large spore-bearing members, and the adaptations to meet them, if successful, would become stereotyped as permanent morphological facts. In *Tmesipteris* also, the normal septum is similar in origin to the sporogenous masses, and is undistinguishable from them while young; thus, from the developmental point of view it may also be looked upon as a result of sterilization. But, conversely, it has been shown that in certain abnormal synangia of *Tmesipteris* the septa may be completely absent, while in others it has been demonstrated that those tissues which normally form the septum may become sporogenous; there is accordingly no absolute and essential difference between tissue of the septum and the sporogenous tissue in the septate synangium of *Tmesipteris*.

Thus, our observations afford answers to the four questions above put forward; but it is true that the evidence is neither over-abundant nor conclusive. Those who best appreciate the greatness of the gulf between the Bryophyta and the Vascular Cryptogams would least expect it to be abundant. Its value is to be estimated in connection with that derived from the Bryophyta; the quotations above given from LEITGEB (p. 487, &c.) show that he deemed that the progress of sterilization in certain series of Liverworts was demonstrated, while comparison leads to the probability of further formation of sterile tissues in such plants as the Anthoceroteæ, in which elater-like cells, similar to those which appear to have undergone consolidation to form the columella, are dispersed through the sporogenous tissue. Somewhat similar evidence, though not so cogent, leads to the conclusion that sterilization, resulting in sterile tissue-masses or isolated sterile cells, has taken place also among the Vascular Cryptogams. Such evidence is of the greatest importance in connection with our hypothesis of the origin of the strobilus from a sporogonial head. While I know of no facts which present a real obstacle to the acceptance of the hypothesis, a large number of facts relating to external form, internal structure, and development, which have been discussed in previous pages, fall in with the theory. In the absence of more extensive and more direct evidence, therefore, the whole question before us must (like so many problems relating to descent) resolve itself in great measure into a balance of probabilities. In view of the facts as a whole, it seems to me at present probable that the strobilus of the *Equisetineæ* and *Lycopodineæ* is the counterpart of a sporogonial head, such as that seen in the Bryophyta; that it attained its present condition by partial sterilization of the originally continuous archesporium, and outgrowth of the isolated parts, together with external protective tissues, as sporangia, while there were also formed, probably simultaneously, appendicular organs (sporangiophores and sporophylls), which bear them. That in certain cases (Psilotaceæ and probably Equisetineæ) the original sporangia underwent a further subdivision, by formation of sterile septa, the result being synangia of various types. *Isoetes*, and probably *Lepidodendron*, are to be taken as examples of such sterilization resulting in trabeculæ in place of complete septa. The sterilization thus involved would be similar in kind to that which was so ably traced by LEITGEB in the Liverworts. A point of special interest in connection with this is the presence of sterile cells in the young sporangia of *Equisetum* and the Psilotaceæ, scattered through the sporogenous masses; similar cells have been observed by ROSTOWZEW ('Recherches sur l'Ophioglossum vulgatum, L.,' Kjöbenhavn, 1891, p. 28, Plate 2, fig. 5) in the Adder's-tongue, and I have been able to confirm the fact. It thus appears that in *Equisetum, Psilotum, Tmesipteris*, and *Ophioglossum*, all types in which the sporangia are closely associated together so as to form synangia, a considerable proportion of the potential sporogenous tissue is sterile, the cells yielding up their substance to nourish their fellows, which develop as mature spores. This cannot be looked upon as a mere coincidence; it demands careful consideration, both from the physiological and morphological aspects.

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* The same is also the case in *Frullania*, where "elaters" of trabecular character, and attached at both ends, are formed from sister cells of those which, after division, give rise to the spores. See HOFMEISTER, 'Higher Cryptogamia' (Plate 12, fig. 9), and LECLERC DU SABLON, 'Ann. Sci. Nat.,' Bot., 7 série, vol. 2, 1885, p. 130, Plate 7.

From the physiological point of view the sterile cells act the part of a diffused tapetum; they become disorganized, and the substances which compose them are taken up into the developing spores. Developmentally they are sister cells with those which produce spores,—they are, in fact, potentially sporogenous cells, and the question may be asked, why they do not develop as such. It would appear that want of nutrition determines the matter, and I think the state of the case is probably as follows: these plants have increased the bulk of their potential sporogenous tissue beyond the point at which it can be wholly matured, and the result is an arrangement by which the number of spores actually produced can be advanced to the largest figure which the plant will be able to ripen. In *Psilotum* it has been distinctly seen that certain cells of the sporogenous mass first assume denser protoplasmic contents, and that the number of these increases up to a certain limit when the sporogenous cells separate from one another; it is probably the condition of the plant at the time as regards nutritive supply which will determine this limit, a larger proportion becoming sporogenous in a well-nourished plant, and a smaller number in an impoverished plant. In this connection, it may be noted that though my specimens of *Psilotum* came from the Glasgow garden, those of *Tmesipteris* were grown in their native country, and both showed the potential sporogenous tissue only partially fertile.

Examining the peculiarity, which these plants share, from the comparative and morphological side, it may be noted that in allied forms, such as *Phylloglossum*, *Lycopodium*, *Selaginella*, *Isoetes*, and in most Filicineæ other than *Ophioglossum*, the large majority, or even all of the cells of the sporogenous mass form spores; a few odd cells may suffer arrest and disorganization, as has been seen in the microsporangia of *Selaginella* and *Isoetes*, but (with the exception of the megasporangia of the latter genera) the arrest and destruction of a considerable proportion of potentially sporogenous cells is not a distinct feature; this makes the matter still more deserving of consideration.

It has been noted that in the *Anthoceroteæ* LEITGEB saw evidence of sterilization of tissues, resulting in the formation of the central columella; in addition to this there are also present in *Anthoceros* sterile elaters which originate with the sporogenous cells from the archesporium; thus *Anthoceros* shows both the result of a more general sterilization as tissue masses, and individual sterilization of cells scattered through the potential sporogenous tissue. Now in *Equisetum*, *Psilotum*, and *Tmesipteris* we see plants with sporangia grouped in such a way as to suggest, on our general hypothesis, an origin by subdivision of simpler sporangia, the septa being a result of partial sterilization; but in addition to this (as also in *Anthoceros*) sterile cells are scattered through the potential sporogenous masses; it is true these cells, in the vascular plants quoted, do not form cell-walls as do the elaters of *Anthoceros*, but morphologically speaking, in both cases we have to deal with sterilized cells of a potential sporogenous mass, and in both cases the organisms concerned are such as give good reason to recognize in the presence of masses of vegetative tissue (columella and septa), the results of previous sterilization. In the presence of these cells scattered through the sporogenous tissue, I should be disposed to recognize that *Equisetum*, *Psilotum*, and *Tmesipteris* show a condition which, with little further modification, might lead to further subdivision of their sporangia; this would be readily effected by the consolidation of such scattered cells into coherent masses, in a manner illustrated by *Metzgeria*, *Aneura*, and the Anthoceroteæ.

It has been noted that *Ophioglossum* shows a similar condition: this interesting fact will be considered in due course when the Filicineæ are under discussion.

If the reasoning brought forward in the above pages be accepted, the strobiloid

Vascular Cryptogams would take a place in the *ascending* series of vascular plants. This was clearly the opinion of NAEGELI. But certain other writers have looked upon them as examples of reduction: thus STRASBURGER ('Bot. Zeit.,' 1873, No. 6, &c.) contemplated it as probable that the sporangia of *Lycopodium* and *Selaginella* were the result of contraction of the whole fertile frond of the Ophioglossaceæ, while the synangium of *Psilotum* represented for him the result of reduction of a whole strobilus of *Lycopodium*. Those also who look upon the Leptosporangiate Ferns as the nearest of living vascular plants to the Bryophyta are often disposed to regard the strobiloid Pteridophyta as comparatively reduced types: and doubtless some will see in the sterile cells scattered through the sporogenous masses of *Equisetum*, *Psilotum*, and *Tmesipteris* evidence of such reduction. It is true the Pteridophyta at present living are smaller than many of the individuals of former ages: but their sporangia do not show evidence of reduction of type, or of coalescence, as compared with their fossil relatives. If the living strobiloid types have been reduced as regards their spore-bearing parts, their relatives, the Calamarieæ and Lepidodendra, must also have been reduced; that is, some of the earliest fossil plants of which we have any accurate knowledge would have to be looked upon as reduced types, and in the descending scale of evolution. This is doubtless possible, but seems to me by no means probable; in fact, it is very much like a *reductio ad absurdum*. Accordingly I conclude on this, as also on grounds of general comparison, that the more probable view is that the strobiloid types, both ancient and modern, are in the ascending scale of evolution, as they must certainly be if our working hypothesis is sound.

I have now examined types of all the genera of living Vascular Cryptogams, exclusive of the Filicineæ. On the latter, rather extensive observations have also been made, but I propose to hold back such results as are already in hand till my investigations of the Filicineæ have been completed. In the meanwhile it may be remarked that the main lines of investigation and of argument pursued in the above pages will be found applicable also to the Filicineæ.

I do not propose to discuss the results from a more general or from a phylogenetic point of view till the close of the remaining part of this Memoir, which will have as its subject the morphology of the spore-bearing members of the Filicineæ.

In conclusion it may be remarked that there appears to be good reason, both from grounds of comparison and from detailed observation, to believe that one at least of the three possible modes of increase in number of spore-producing masses (separate archesporia) suggested in the introductory paragraphs (p. 484), has played a part in the evolution of Vascular Cryptogams, viz., subdivision and partitioning of an originally simple sporogenous mass, by its partial sterilization and formation of septa. It is not contended that the point has been actually demonstrated, but the facts derived from the study of *Tmesipteris*, when compared with those relating to other Lycopods, and *Isoetes*, make this conclusion appear a probable one. It may remain an open question how important a part this factor may actually have taken in the evolution of vascular plants: my own opinion is that subdivision has largely, though not exclusively, been the means of increase in number of separate archesporia. But at least I think that both the general considerations and the detailed facts above discussed go far to show that progressive sterilization and partitioning of spore-bearing members are factors which will have to be taken into account in solving the problems of origin and progress of vascular plants.

DESCRIPTION OF FIGURES.

PLATE 42.

Equisetum arvense, L.

Fig. 1. Radial longitudinal section of part of a young strobilus, showing two sporangiophores in a very young state. (× 300.)

Fig. 2. Part of an older sporangiophore in radial section, with young sporangium: the group of cells shaded corresponds to the cell shaded in fig. 1. (× 300.)

Fig. 3. Ditto, showing the first periclinal division in the outer cell. (× 300.)

Fig. 4. Ditto; considerably older, and showing cells (×) which are added to the archesporium as the result of subdivision of the outer of the two original cells. (× 300.)

Fig. 5. Ditto; older. Cells marked (×) correspond to those in the previous figure. (× 300.)

Fig. 6. Ditto; a good deal older. All the essential parts of the sporangium are here initiated. (× 300.)

Fig. 7. Oblique section through a sporangiophore of age corresponding to fig. 4, so as to pass through the axis of the young sporangium in a plane at right angles to that of fig. 4. (× 300.)

Fig. 8. A section similar to fig. 7. (× 300.)

Fig. 9. Transverse section through a sporangium of age corresponding to that shown in fig. 6. (× 300.) The arrow indicates the side next to the stalk of the sporangiophore.

Equisetum limosum, L.

Fig. 10. Part of a tangential section of a strobilus, which traverses the sporangiophores transversely. *sp.* = stalks of sporangiophores. *a, b, c* = three sporangia cut transversely, and showing extreme differences of size and complexity in sporangia side by side. (× 300.)

Figs. 11, 12, 13. Three sporangia from the same strobilus, cut in median longitudinal section, and showing different types of segmentation, together with difference of bulk. (× 300.)

Fig. 14. Median section of a rather older sporangium, from near the apex of a strobilus. *v.b.* shows where the vascular bundle is beginning to be developed. (× 300.)

PLATE 43.

Fig. 15. Median longitudinal section of a sporangium at the base of the strobilus, together with the annulus (*a.*). (× 300.)

Fig. 16. Tangential section of a sporangium of same age as figs. 11–13. (× 300.) Compare fig. 11.

Figs. 17, 18. Ditto; more complex specimens. (× 300.)

Fig. 19. Tangential section of a sporangium in a more advanced state. (× 300.)

Fig. 20. Apex of an older sporangium in radial section. The tapetum (*t*) is now clearly defined. (× 300.)

Fig. 21. Part of an older sporangium, showing the tapetum (*t.*) still a clearly-defined band, though the individuality of the cells is lost; within this the sporogenous tissue, of which certain cells (*a*) are abortive. (× 300.)

Phylloglossum Drummondii, Kunze.

Fig. 22. A plant of *Phylloglossum,* showing tuber-leaves and strobilus; one sporophyll of the latter is at a distance below the rest, intercalary growth having taken place in the axis above it. (× 3.)

Fig. 23. A plant of *Phylloglossum* grown in the Glasgow Botanic Garden; the strobilus is branched into two unequal parts. (× 3.)

Fig. 24. Median longitudinal section through the plant represented as fig. 8 in 'Phil. Trans.,' 1885, Plate 71. *a.* = apex; *l.* = leaf (protophyll); *r.* = root. (× 150.)

Fig. 25 (i., ii., iii.) Successive transverse sections of the young leaf (protophyll) of the plant represented as fig. 10 in 'Phil. Trans.,' 1885, Plate 71. (× 150.)

PLATE 44.

Fig. 26. Apex of a strobilus in median longitudinal section showing an initial cell (*i*), two sporophylls (*l′ l″*), the latter just beginning to be developed; in connection with *l′* is a sporangium, of which the archesporium (*a*) consists apparently of one cell. (× 325.)

Fig. 27. Another section from the same sporangium, showing further segmentations, which may have been present in the section shown in fig. 26, but made invisible by the method of clearing used. (× 325.)

Fig. 28. A slightly older sporangium in radial section. (× 325.)

Fig. 29. An older sporangium, in which periclinal divisions have begun in the cells of the wall of the sporangium. (× 325.)

Fig. 30. Radial section of a sporangium, in which the sporogenous cells are beginning to separate, but the tapetum is not yet formed from the inner layer of the wall. (× 150.)

Fig. 31. Transverse section of a young sporangium. (× 300.)

Fig. 32. Transverse section of a sporangium, of which one-half is shown; the stage is slightly younger than that of fig 30. (× 300.)

Fig. 33. Tangential section of a sporangium, of which rather more than one half is shown; the asterisk indicates the middle of the sporangium. (× 325.)

Lycopodium Selago, L.

Fig. 34. Radial section through a sporophyll (*l*) at the base of which a sporangium is beginning to make its appearance as a slight swelling. (× 300.)

Fig. 35. A similar sporangium, in radial section, rather more advanced. (× 300.)

Fig. 36. Ditto, older; the archesporium is shaded. (× 300.)

Fig. 37. Ditto, a more advanced stage; showing very regular segmentation. (×300.)

Fig. 38. Ditto, showing a less regular type of segmentation. (× 300.)

Fig. 39. Ditto; still less regular. (× 300.)

Fig. 40. Ditto, older; the tapetum (*t.*) not yet complete. (× 150.)

Fig. 41. Ditto, older; showing the spore-mother-cells separated from one another, but not yet divided into tetrads. (× 150.)

PLATE 45.

Fig. 42. Tangential section of a young sporangium of *L. Selago;* the cells numbered i., ii., iii., correspond to those similarly numbered in fig. 36 (× 300.)

Fig. 43. Ditto, older. (× 300.)

Fig. 44. A small part of a similar section from a rather older sporangium. (× 300.)

Fig. 45. Young sporangium, seen in superficial view. (× 300.) *st.* = stem; *l.* = sporophyll.

Fig. 46. A sporangium of almost the same age seen in transverse section; compare the line in fig. 42; the archesporial cells are shaded in both figures, and numbered (ii.). (× 300.)

Fig. 47. Ditto. (× 300.)

Fig. 48. Ditto, older, before the tapetum is defined. (× 300.)

Fig. 49. Ditto; half of an older sporangium in which the formation of the tapetum (*t.*) is almost complete. (× 300.)

Lycopodium Phlegmaria, L.

Fig. 50. Tangential section of a young sporangium, showing the archesporium, referable to not more than four, and possibly to two cells. (× 300.)

Lycopodium carinatum, Desv.

Fig. 51. Transverse section of a sporangium, so as to traverse the sub-archesporial pad (*s.p.*); the two ends of the curved mass of sporogenous tissue are cut through, and are shaded; this is intended for comparison with a transverse section of the "fertile frond" of *Ophioglossum*. (× 300.)

Lycopodium dichotomum, Jacq.

Fig. 52. Part of the wall of sporangium in section; the tapetum is shaded. (×150.)

Fig. 53. The same, showing the point of dehiscence. (× 150.)

Lycopodium inundatum, L.

Fig. 54. Radial section of a young sporangium, showing periclinal division in two distinct cells; two archesporial cells are shaded. (× 300.)

Fig. 55. A similar section of an older sporangium. (× 300.)

Lycopodium clavatum, L.

Fig. 56. Radial section through a very young sporangium, showing the first periclinal division. (× 300.)

Fig. 57. Ditto, showing periclinal divisions in two distinct cells. (× 300.)

Fig. 58. Ditto, older, showing result of periclinal division in three cells; the archesporium thus defined is shaded. (× 300.)

Fig. 59. Older sporangium, in radial section, with large sporogenous tissue, so grouped as to be still referable to three original cells; compare fig. 58. (× 300.)

PLATE 46.

Fig. 60. Radial section of an older sporangium; *st.* = the adaxial side: the sporogenous tissue not shaded, it is still referable to the three parent cells, the lower limit of the groups being here unusually irregular. The tapetum is shaded. (× 300).

Fig. 61. Radial section of a sporangium, which shows early periclinal divisions of the superficial cells; the fate of the inner cells (*o*, *o*) is uncertain; *v.b.* = vascular bundle. (× 300.)

Fig. 62. Ditto. (× 300.)

Fig. 63. Tangential section of a sporophyll bearing a sporangium of age corresponding to that in fig. 56; the periclinal walls have not yet appeared in all the parent cells of the sporangium. (× 300.)

Fig. 64. A similar section of an older sporangium; in both of these the archesporium is shaded. (× 300.)

Fig. 65. Part of a tangential section of an older sporangium; *t.* = tapetum; *v.b.* = vascular bundle; *s.a.* = sub-archesporial pad; sporogenous tissue is deeply shaded. (× 300.)

Fig. 66. Small part of the sub-archesporial tissue, showing a process rising upwards into the mass of spore-mother-cells. (× 300.)

Fig. 67. A similar part from an almost mature sporangium; the irregular upward processes are now partly disorganized. (× 150.)

Fig. 68. View of the superficial cell-net of a sporangium, as seen from above. (× 300.)

Fig. 69. Transverse section of such a sporangium traversing the archesporium, which is shaded. (× 300.)

Fig. 70. Transverse section of an older sporangium; the three rows of parent cells of the sporogenous tissue may be still recognized. (× 300.)

Lycopodium alpinum, L.

Fig. 71. Radial section through a sporophyll and young sporangium. (× 300.)

Fig. 72. Ditto, the archesporium shaded. (× 300.)

Fig. 73. Ditto, rather older. (× 300.)

Fig. 74. Ditto, the cells marked (×) have apparently been derived by extra periclinal divisions from the superficial cells. (× 300.)

Fig. 75. Radial section of an older sporangium in which the spore-mother-cells are about to separate. The vascular bundle shows a slight extension upwards into the stalk of the sporangium. (× 150.)

PLATE 47.

Fig. 76. Tangential section through a young sporangium, showing an archesporium consisting of twelve cells, which are shaded. (× 300.)

Fig. 77. An upgrowth of the sub-archesporial tissue as a process, which projects between the sporogenous cells. (× 300.)

Selaginella Martensii, SPRING.

Fig. 78. Radial section, including apex (*ap.*), and traversing a young sporophyll (*l*) and sporangium (*x*). (× 550.)

Fig. 79. Ditto, rather older. (× 550.)

Selaginella spinosa, P.B.

Fig. 80. Radial section through a very young sporangium. (× 550.)

Fig. 81. Ditto. (× 550.)

Fig. 82. Ditto. (× 550.)

Fig. 83. Ditto. (× 550.)

Figs. 84–86. Ditto, older. (× 550.)

Fig. 87. Ditto, a good deal older, showing all the essential parts of the sporangium together with ligule, and part of sporophyll. (× 300.)

Fig. 88. Tangential section of a sporangium of about the same age as figs. 84–86 : the archesporium is referable apparently to four parent cells. (× 550.)

Figs. 89–90. Transverse sections of sporangia of two different ages. *l.* = ligule, *t.* = tapetum, *sp.* = sporogenous tissue. (× 300.)

Fig. 91. Radial section of a megasporangium showing the single tetrad still very small, and the rest of the potential sporogenous cells arrested. (× 150.)

Fig. 92. *a–w.* Low-power drawings, showing outlines of the sporangia of various species, in radial, tangential, and transverse sections, together with parts of the sporophylls : *a, b, c, Phylloglossum Drummondii; d, e, f, L. Selago; g, h, i, L. phlegmaria; k, l, m, L. inundatum; n, o, p, L. carinatum; q, r, s, L. alpinum; t, u, v, w, L. clavatum.* (× 18.)

PLATE 48.

Lepidostrobus Brownii, SCHPR.

Fig. 93. Wall of sporangium from a tangential section of the cone (No. 7 in the Museum series of tangential sections) : it shows the outer sclerotic series of cells (*scl.*), with several layers of thin-walled cells within. (× 150.)

Fig. 94. From a photograph of part of a transverse section of the cone, showing three sporangia, with the upward projecting sub-archesporial pad as a median ridge (*r.*). (× 4½.)

Fig. 95. From a photograph of a tangential section of the cone.

Fig. 96. Drawing of a sporangium in tangential section of the cone with its sporophyll (*sp.*), slightly diagrammatic. *r.* = sub-archesporial ridge ; *v.b.* = vascular bundle ; *p* = processes rising from the ridge. (× 8.)

Fig. 97. Part of a radial section of the cone showing a small part of the base of the sporangium; *r.r.* = the sub-archesporial ridge, together with the processes (*p.p.*) which rise from it. (× 40.)

Fig. 98. The ridge (*r.*) as seen in tangential section of the cone (compare figs. 95, 96), showing on a larger scale the processes (*p.*) which project far upwards into the mass of spores. (× 40.)

Fig. 99. A sporangium from the apex of the cone, cut tangentially (compare fig. 95). The sporangium was not fully matured, and showed very large processes (*p*) springing from the sub-archesporial ridge, and continuous upwards towards the upper wall of the sporangium. (× 40.)

Fig. 100. Another such, with its sporophyll. (× 40.) Figs. 99 and 100 are taken from slide No. 9 of the tangential series in the British Museum.

Lepidostrobus, sp., Hough Hill.

Fig. 101. From a photograph of a *Lepidostrobus* from Hough Hill, supplied by Mr. Lomax, and cut tangentially. The sporophylls and sporangia are easily seen, while each sporangium shows a dark process rising from the slightly convex sub-archesporial pad, and extending far upwards into the sporogenous mass. (× 4½.)

Fig. 102. The base of one of these processes seen under a higher power, and showing the cellular structure of the lower part, though this structure is lost upwards. (× 150.)

Lepidodendron Brownii, Schpr.

Fig. 103. Similar section from Schimper's smaller cone, in the British Museum, showing ridge (*r.*) and processes (*p.p.*) (× 20.)

PLATE 49.

Isoetes lacustris, L.

L. = ligule; *v.* = velum; *t.* = tapetum; *tr.* = trabeculæ; *sp.* = sporogenous tissue; *v.b.* = vascular bundle.

Fig. 104. Part of radial section of a plant which has traversed a young leaf in median longitudinal section, the upper (adaxial) surface bears a rather regular layer of cells, as yet not divided periclinally; these are the parent cells of the sporangium. (× 300.)

Fig. 105. These cells are represented in an older state, having divided by both periclinal and anticlinal walls; the inner archesporial cells are shaded. (× 300.)

Fig. 106. A similar section, showing addition of cells (×) resulting from repeated periclinal division of superficial cells to the archesporium. (× 300.)

Figs. 107, 108. Older sporangia with archesporium shaded. (×) = cells believed to have been added by subsequent periclinal division of superficial cells. (× 300.)

Fig. 109. A much older sporangium, already developing as a microsporangium, in similar section, showing the sporogenous tissue as a connected and undifferentiated band. (× 300.)

Fig. 110. Part of an older microsporangium, in similar section, showing the potential archesporium differentiated into trabeculæ (*tr.*) and sporogenous masses (*sp.*), while the tapetum is also clearly defined : at (*) is an extra periclinal division in the wall. (× 150.)

Fig. 111. Transverse section of a sporophyll and microsporangium ; *v.b.* = vascular bundle of sporophyll. Compare tangential sections of sporangia of *Lycopodium* (figs. 33, 43, 64, 65). (× 150.)

Fig. 112. A microsporangium drawn under low power to show the irregularity of the trabeculæ. (× 8.)

Fig. 113. Shows the structure of the trabeculæ, as well as their irregularity; the superficial layer has developed as a tapetum, which is shaded. (× 150.)

Fig. 114. A microsporangium in longitudinal section. (× 20.)

Fig. 115. The base of one of the trabeculæ of an almost mature microsporangium, still showing cell-structure in its lower part, but disorganized above. (× 150.) Compare fig. 102 of *Lepidostrobus.*

Fig. 116. Transverse section of a sporophyll with a megasporangium, from which the spores have been removed ; the trabeculæ are apparently regular.

Fig. 117, *a* and *b*. A megasporangium which has been so cut as to remove the upper wall (*a*), from which the trabeculæ project into the cavity of the sporangium ; (*b*) is the remainder of the sporangium, *r.* = the ridge, or sub-archesporial pad, which is to be compared with the similar part in *Lepidostrobus* (fig. 94, *r.*) ; it is from this ridge that the irregularly disposed trabeculæ arise. (× 4.)

PLATE 50.

Tmesipteris tannensis, Bernh.

Fig. 118. Median longitudinal section of the apex of a strongly growing stem, showing an initial cell (*x*), but a rather irregular disposition of the segments. (× 150.)

Fig. 119. Apical meristem of the axis of *Tmesipteris* as seen from above: (x) = initial cell, (o) = secondary initials. (× 150.)

Figs. 120 (A and B), 121. Young leaves, in radial section of a bud, showing the way in which they originate on the axis. (× 150.)

Fig. 122. A young leaf as seen in transverse section of the axis. (× 150.)

Fig. 123. A more advanced leaf, probably vegetative; at all events it shows as yet no clear indication of bearing a synangium. (× 150.)

Fig. 124. A very young synangium arising on the adaxial surface of a leaf which is closely similar to fig. 123. In this figure, as also in figs. 120–123, the basal line is more heavily marked. Compare the later figures also. (× 150.)

Fig. 125. Sporophyll bearing a much older synangium; the apical cell (x) may still be seen; the basal line is darkly marked as before, and the sporogenous masses are shaded. (× 150.)

Fig. 125, *bis.* Another specimen of the same, showing very regular disposition of the tissues. (× 150.)

Fig. 126. An older synangium in radial section. (× 150.)

Fig. 127. A vertical section along a line x, x, as shown in fig. 125; l, l are the leaf-lobes. (× 150.)

Figs. 128–130. Transverse sections of sporophylls of successive ages, so cut as to traverse the lower sporangium. l, l = leaf-lobes in fig. 130. (× 150.)

Fig. 131. Transverse section of an older sporangium. (× 150.)

PLATE 51.

Fig. 131, *bis.*, *a–i*, spores from one normal synangium of *Tmesipteris*; *a* is the usual type; *b–i* show various abnormal forms, which appear to result from incomplete division of the tetrads.

Lepidostrobus, sp.

Fig. 132. From a photograph of a transverse section of a strobilus, showing part of two sporangia, which have been traversed in a plane above the sub-archesporial pad, but so as to cut through the sterile projections. These take the form of plates, which appear as dark streaks (*st.*), continuous for a considerable distance in a radial direction through the sporangium. There may be one such streak or plate of sterile tissue, as in the lower sporangium of fig. 132, or two less regular ones, as in the upper sporangium. The section shown in this figure has been slightly oblique: *sp.* = spores almost mature.

Fig. 133. A similar section showing three sterile plates (*st.*), which projected upwards into the mass of spores (*sp.*).

Psilotum triquetrum, Sw.

Fig. 134. Median longitudinal section of a sporophyll. (× 150.) Compare figs. 124 and 125 of *Tmesipteris*.
Fig. 135. Vertical section of a very young synangium, so as to traverse one of the three loculi. (× 150.)
Fig. 136. Ditto, older. (× 150.)
Fig. 137. Ditto, older. (× 150.)
Fig. 138. Ditto, older, on a lower scale. (× 100.) The cells shaded are the actual sporogenous cells.
Fig. 139. Transverse section of a synangium, rather older than that in fig. 135. (× 150.) *l*, *l* = leaf-lobes.
Fig. 140. Ditto, older. (× 150.)
Fig. 141. Ditto, one sporangium. (× 150.)
Fig. 142. Ditto, older. (× 150.)
Figs. 143, 144 illustrate the disorganization of certain cells of the sporogenous tissue, without forming spores. (× 150.)
Fig. 145. Transverse section through a sporangiferous bud of *Tmesipteris*. *ax.* = axis, *f.* = foliage leaves, *l.* = lateral lobes, *sy.* = synangia. (× 20.)

PLATE 52.

Tmesipteris tannensis, Bernh.

Fig. 146. Part of a radial section through a mature synangium, showing the groove between the sporangia, and the insertion of the septum. (× 150.)
Fig. 147. Radial section through a mature synangium, showing the vascular bundles. (× 4.)
Fig. 148. Section in the plane of the septum, showing the course of the vascular branches up the margin of the septum. (× 4.)
Fig. 149. A "double leaf," with abortive synangium (*sy.*). (× 2.)
Fig. 150. A synangium with the upper loculus abortive. (× 2.)
Fig. 151. Ditto, with lower loculus abortive. (× 2.)
Fig. 152. Ditto, with correlative growth, in place of the abortive synangium, inserted on adaxial face. (× 2.)
Fig. 153. Abnormal sporangiophore (*a*) in lateral, (*b*) in abaxial, (*c*) in adaxial view; *sy.* probably represents the abortive synangium. (× 2.)
Fig. 154. A normal sporangiophore from the middle of a fertile zone. (× 2.)
Fig. 155. A sporangiophore from the limit of a fertile zone, with very small leaf lobes. (× 2.)

Fig. 156. A sporangiophore with trilocular synangium. (× 2.)

Fig. 157. Ditto, but less regular. (× $2\frac{1}{2}$.)

Fig. 158. Ditto, with synangium showing no transverse groove. (× 2.)

Fig. 159. Ditto, of type shown in section in fig. 164. (× 3.)

Fig. 160. Ditto, synangium of spherical form, shown in section in fig. 168. (× 3.)

Fig. 161. Median section through a synangium of type shown in fig. 158, with continuous sporogenous mass.

Fig. 162. Detailed drawing from a similar section, showing the tissue, where the septum should normally be present, developing as sporogenous cells (*s.*) and tapetum (*t.*). (× 150.)

Fig. 163. Synangium similar to fig. 161, rather more advanced.

Fig. 164. Synangium similar to that of fig. 159 in radial section, showing no septum; the cavity is filled with sporogenous and tapetal cells.

Fig. 165. Part of these contents drawn in detail from another section of the same series; the line *x*, *x*, shows where the septum would normally be, while a chain of sporogenous cells stretches continuously across it. (× 150.)

Figs. 166, 167. Two transverse sections, the one (fig. 167) higher up, the other (fig. 166) lower down in the same synangium. Fig. 166 shows no septum. Fig. 167 shows a septum cut through, which, therefore, only extended part way downwards into the cavity, from the upper wall of the synangium.

Fig. 168. Transverse section through the spherical synangium shown in fig. 160. No septum is present.

The figs. 132, 133, 161, 163, 164, 166–168 are from photographs kindly prepared for me by Mr. J. Reid.

In conclusion, I wish to acknowledge the kindness of many friends, in contributing supplies of material for this and other kindred investigations. Some of these supplies have been already mentioned in the above pages. I cannot here give a complete list, but wish especially to mention the repeated kindness of Baron von Müller, in forwarding parcels of *Phylloglossum Drummondii*, and to express thanks to him, and to all other donors.

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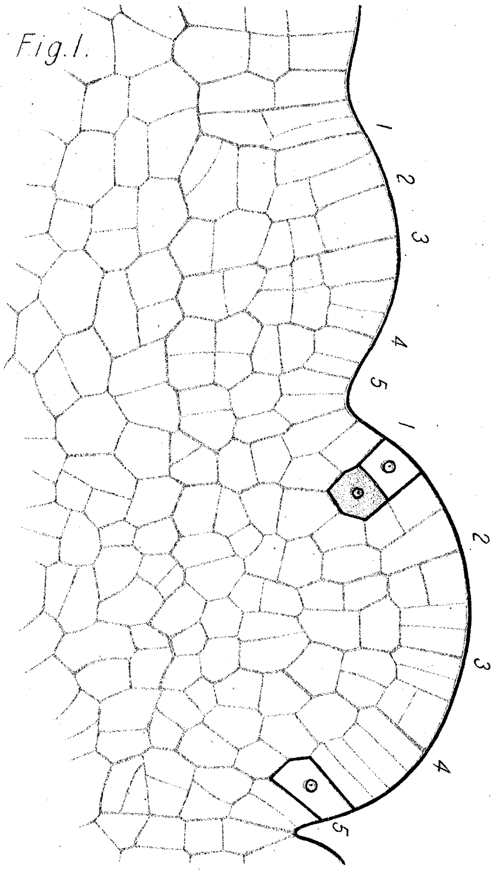
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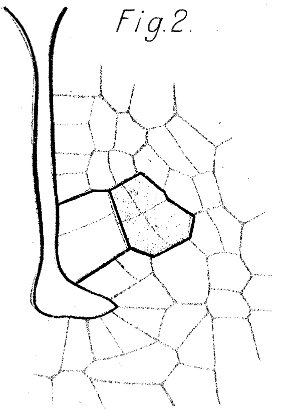

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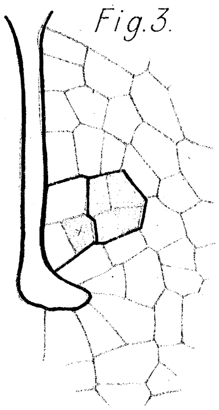

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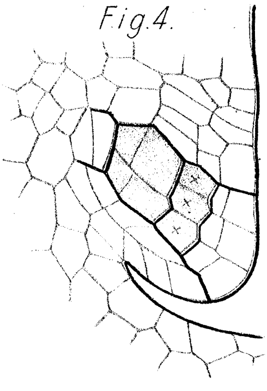

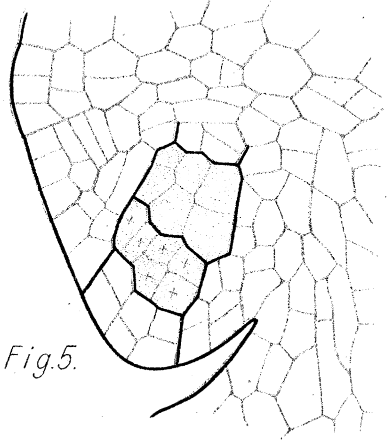

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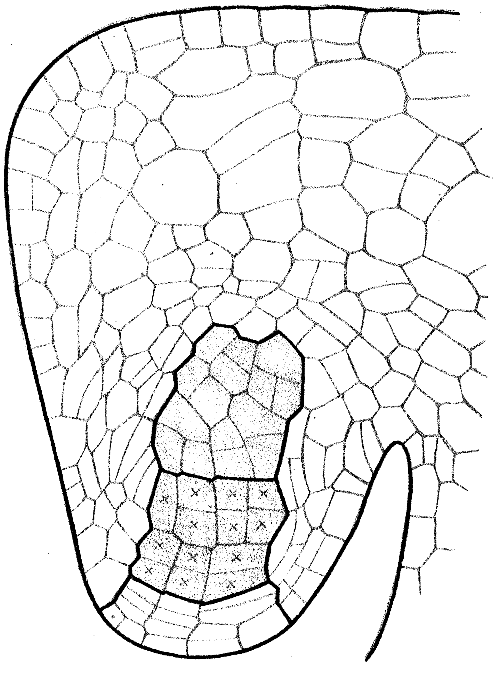

Fig. 6.

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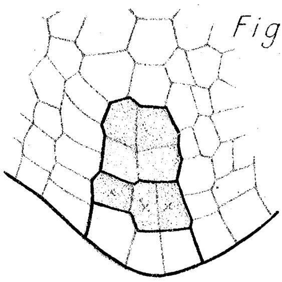

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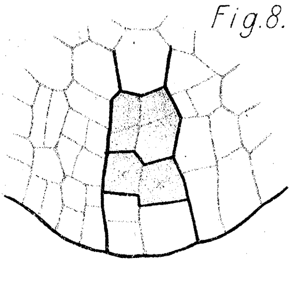

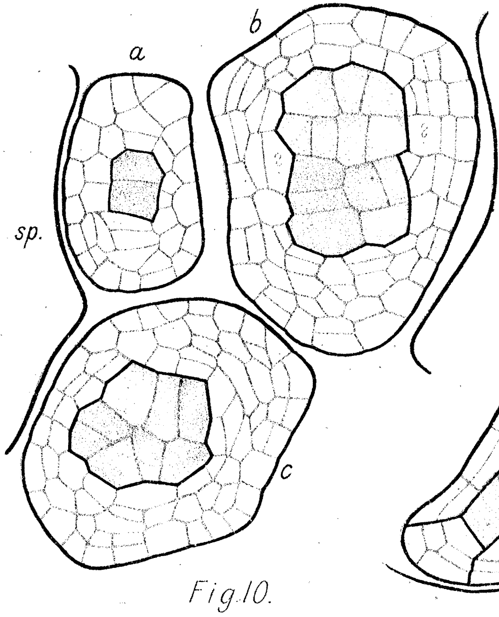

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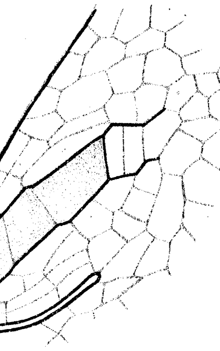

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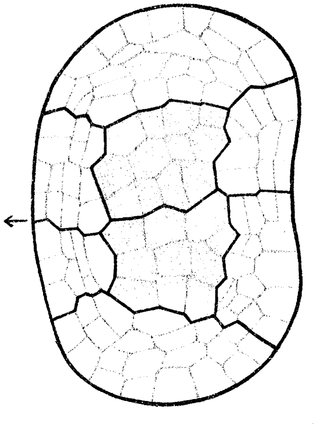

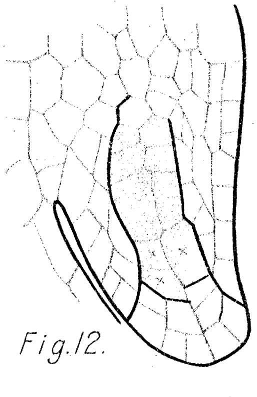

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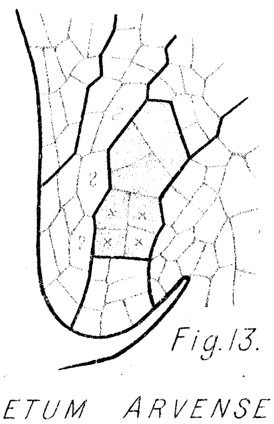

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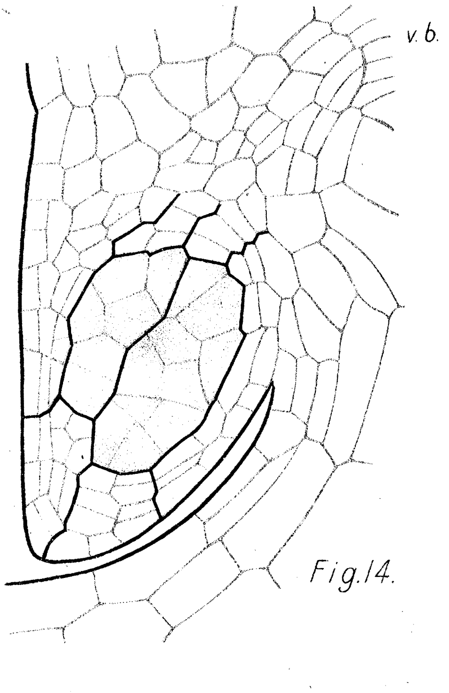

Fig. 14.

Figs 1 – 9. EQUISETUM ARVENSE. L.
Figs 10–14. „ LIMOSUM. L.

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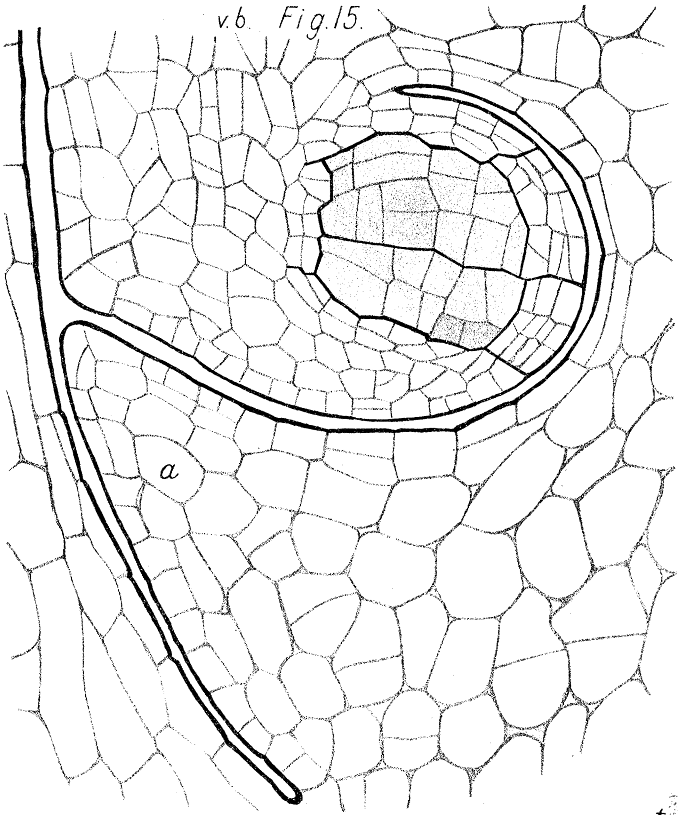
Fig. 15.



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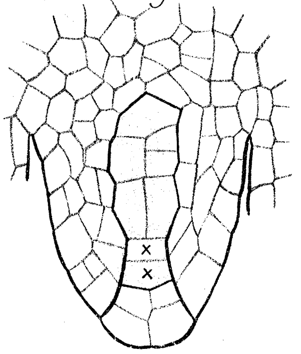

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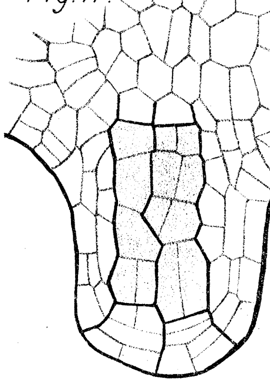

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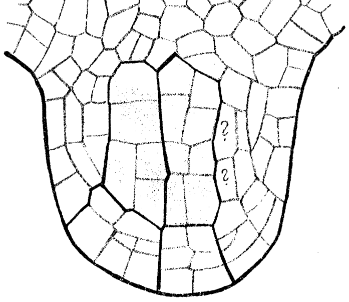

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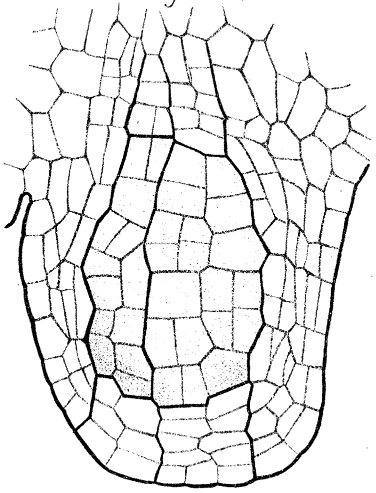

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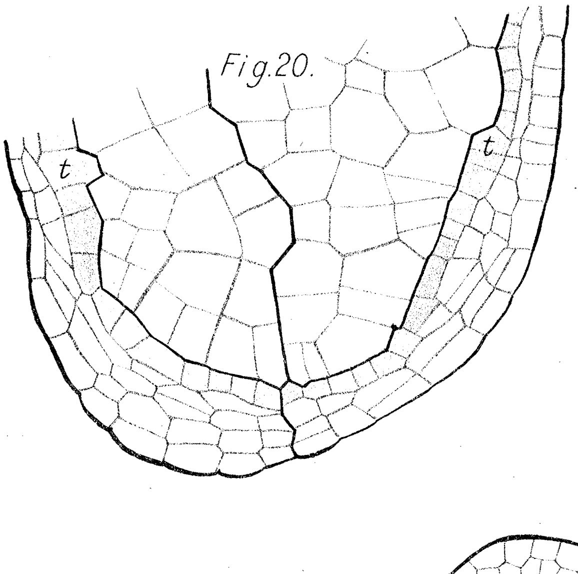

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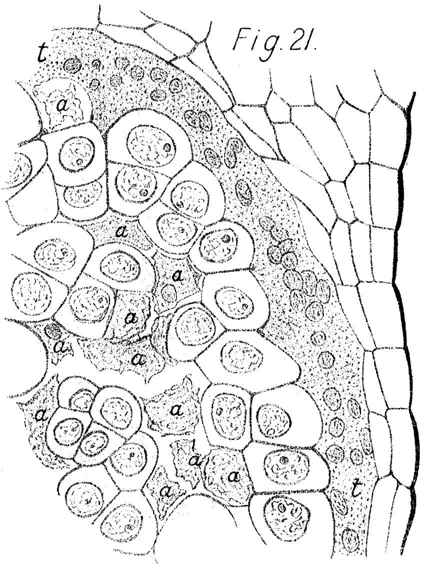
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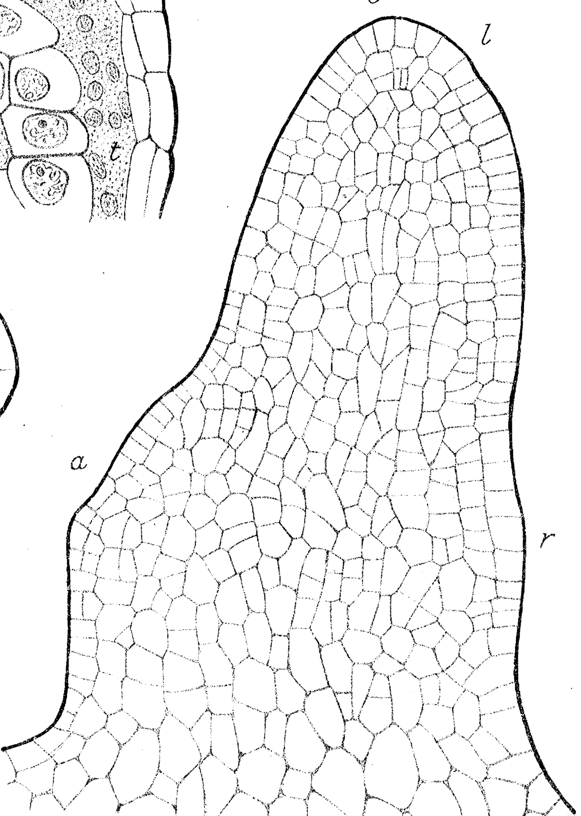

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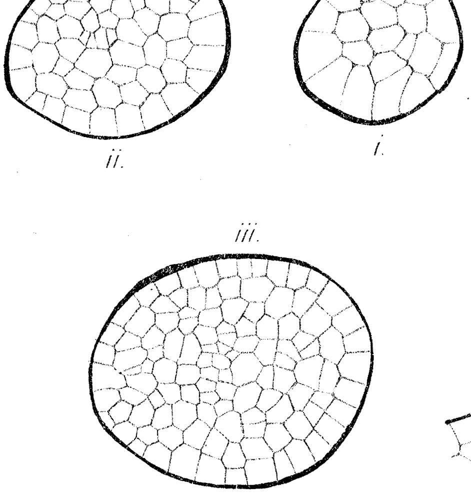

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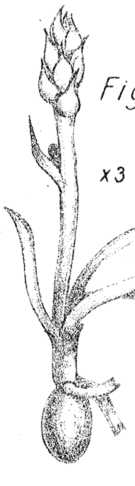

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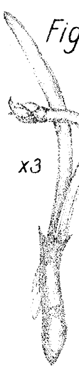

Figs. 15-21. EQUISETUM LIMOSUM. L.

Figs. 22-24. PHYLLOGLOSSUM DRUMMONDII. KUNZE.

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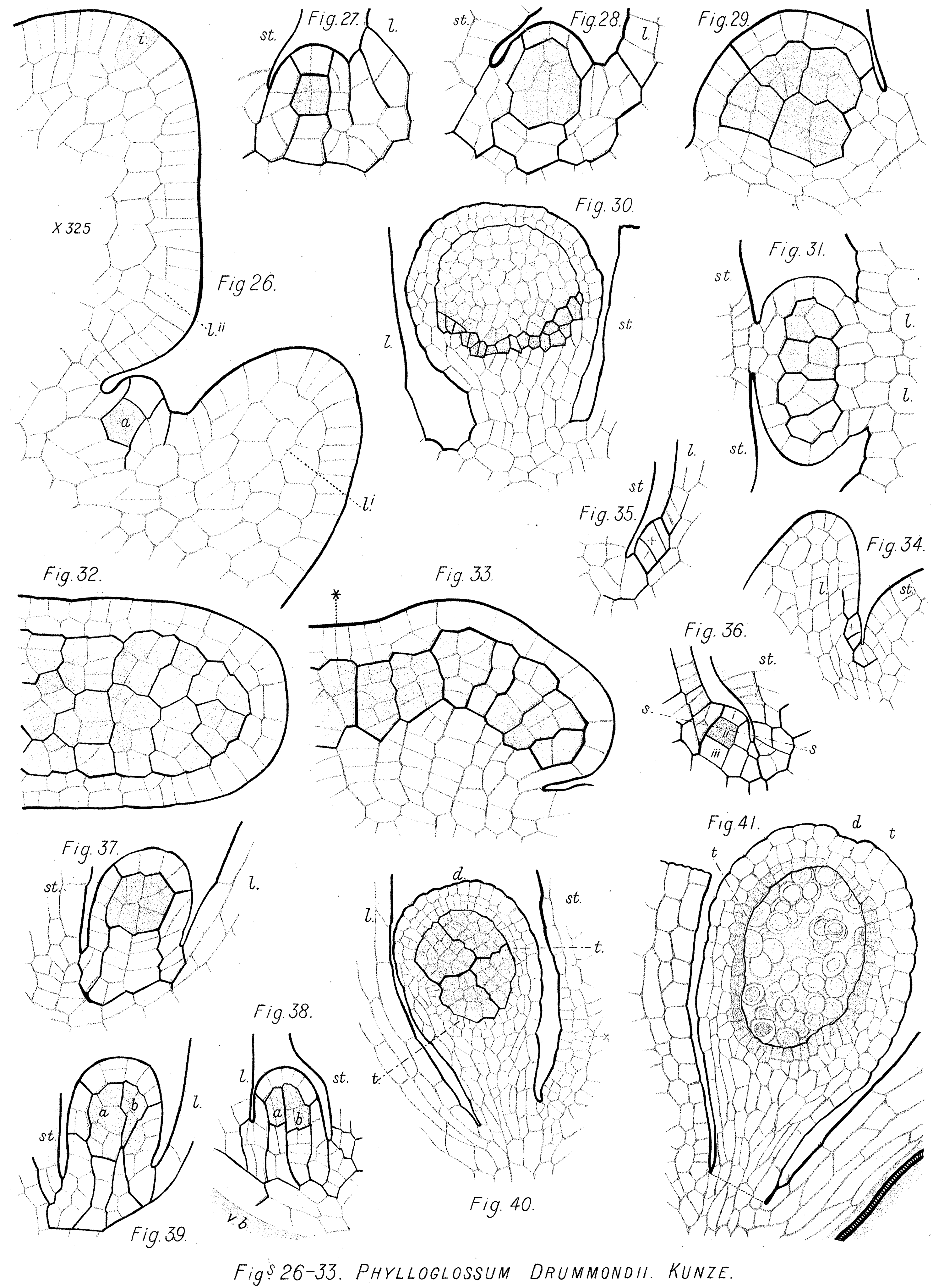
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Figs 26-33. PHYLLOGLOSSUM DRUMMONDII. KUNZE.

Figs 34-41. LYCOPODIUM SELAGO. L.

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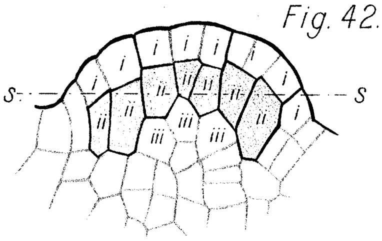

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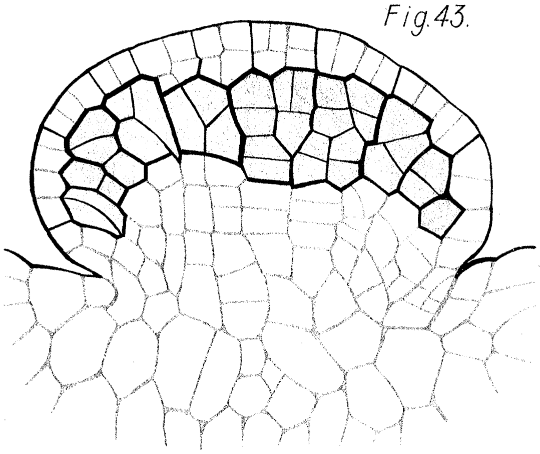

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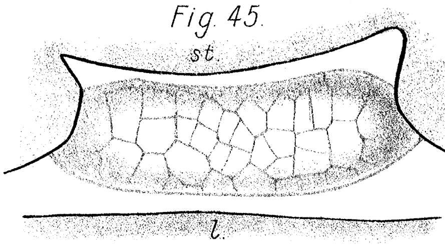

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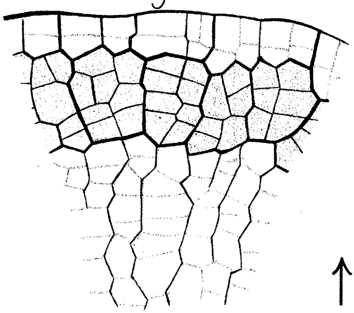

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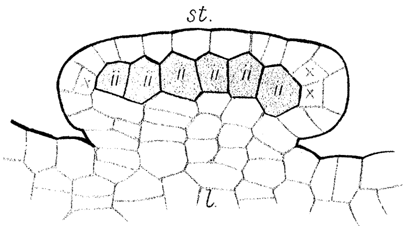

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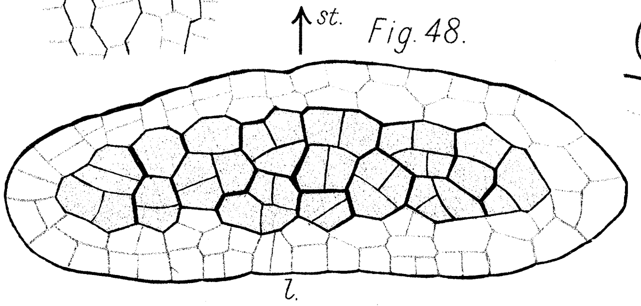

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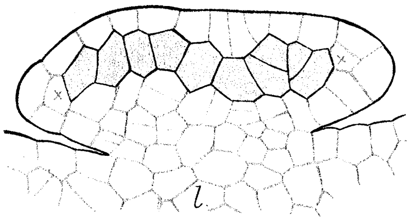

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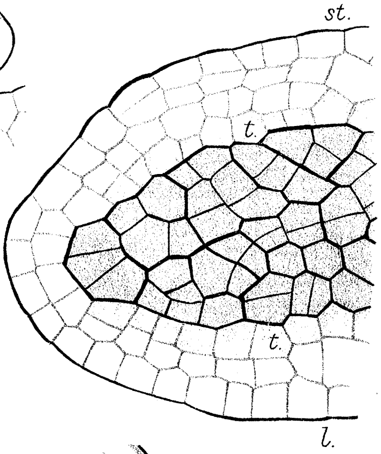

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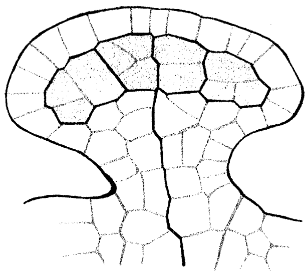

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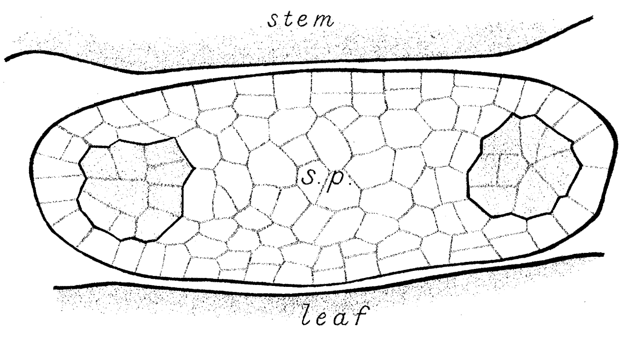
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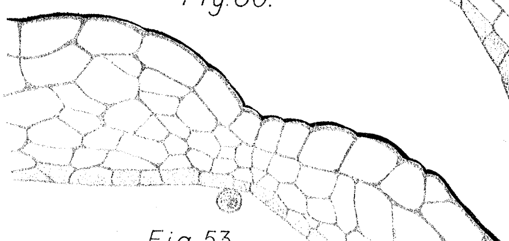
Fig. 51.



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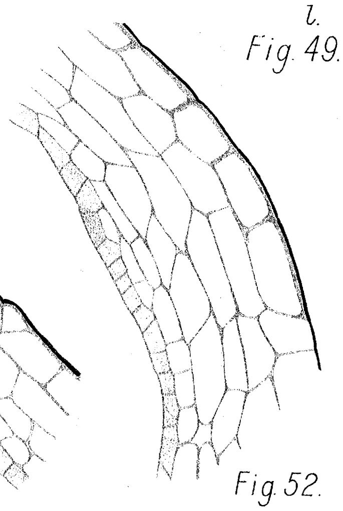

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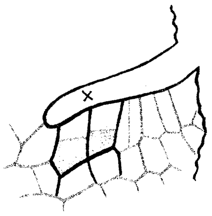

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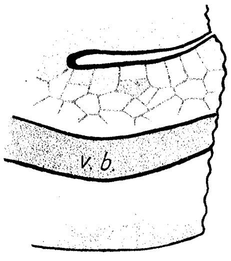

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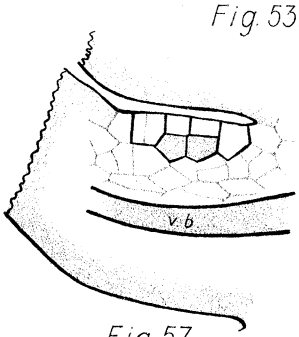

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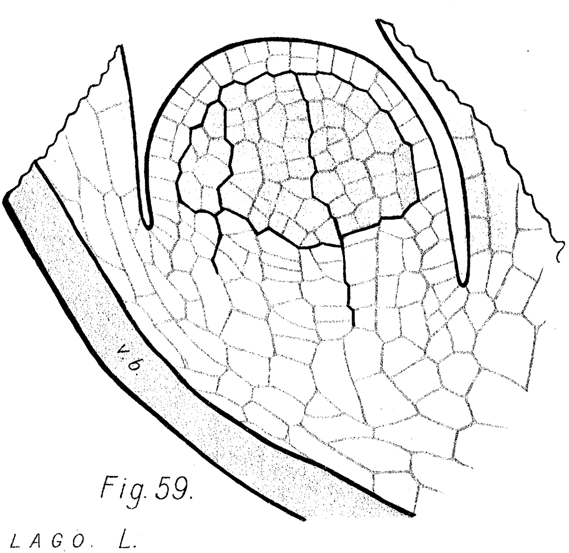

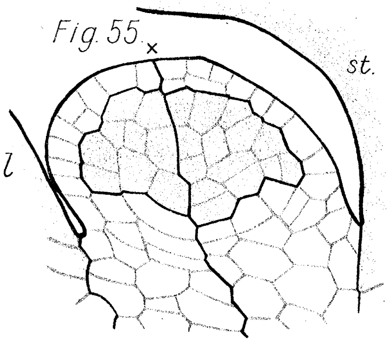

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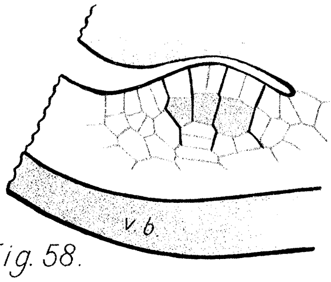
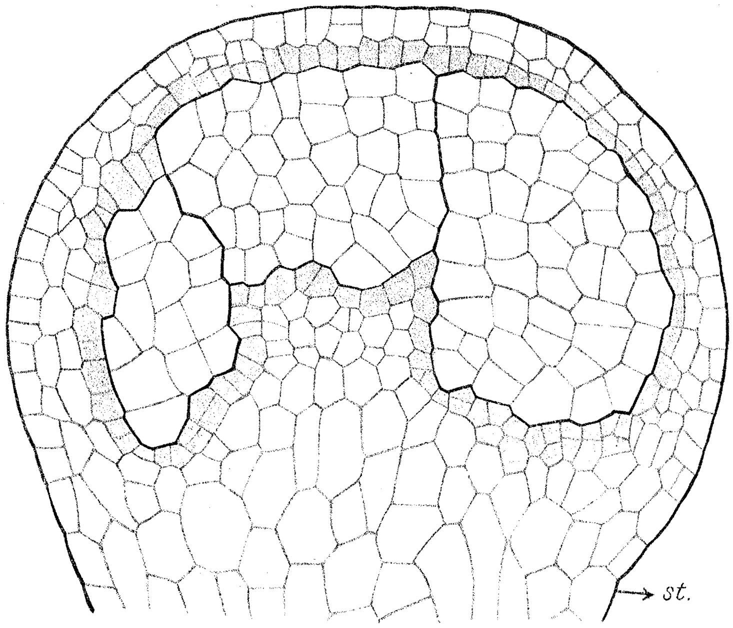


Fig. 58.

Fig. 59.

Figs 42–49. LYCOPODIUM SELAGO. L.
Fig. 50. L. PHLEGMARIA L. Fig. 51. L. CARINATUM DESV.
Figs 52–53. L. DICHOTOMUM JAGQ. Figs 54–55. L. INUNDATUM L.
Figs 56–59. L. CLAVATUM L.



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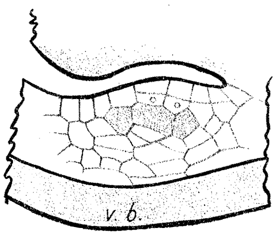

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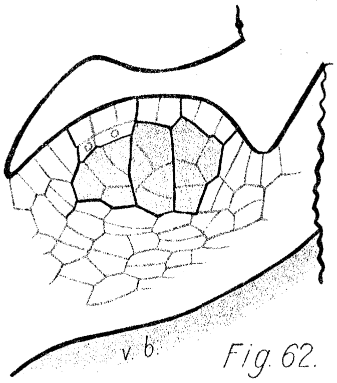

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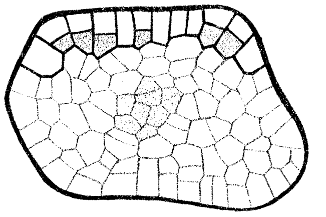

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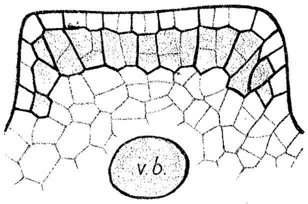

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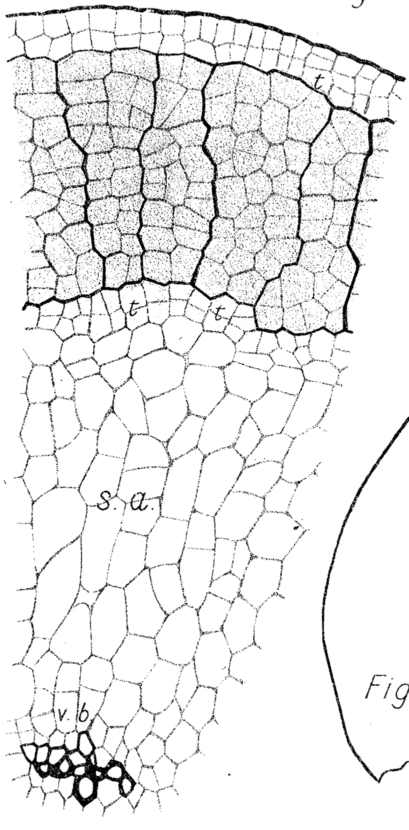

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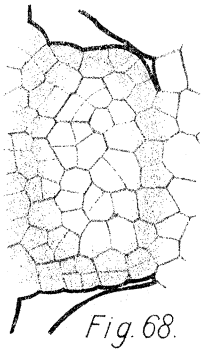

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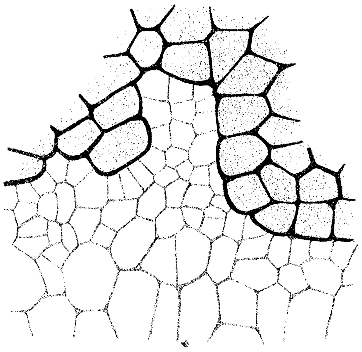

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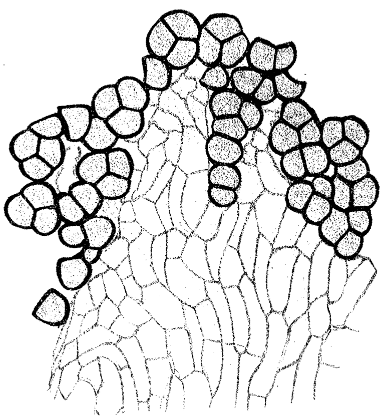

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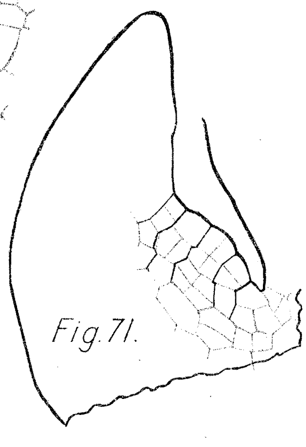

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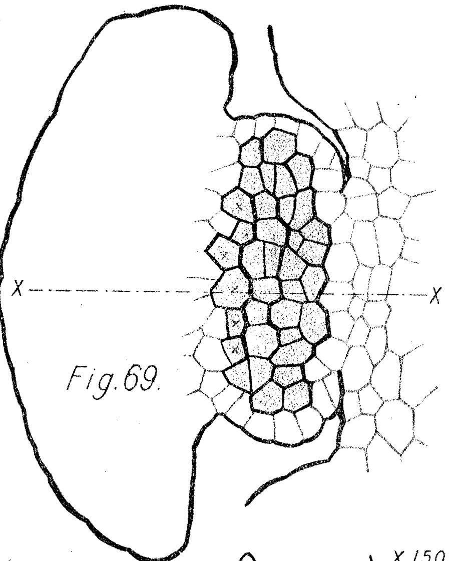
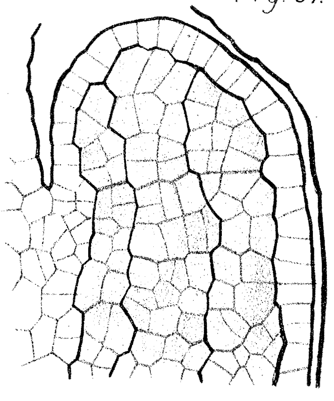


Fig. 69.



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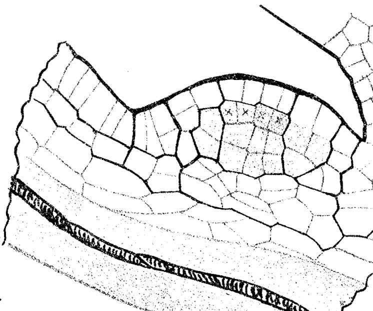

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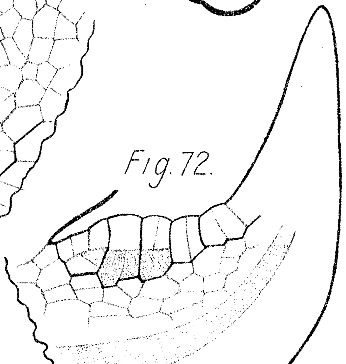

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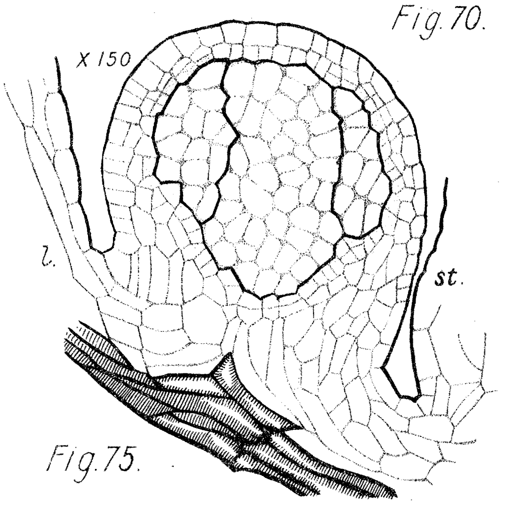

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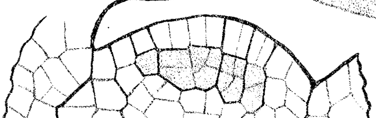

Fig. 73.

Figs 60 – 70. LYCOPODIUM CLAVATUM. L.
Figs 71 – 75. " ALPINUM. L.

Bower del.

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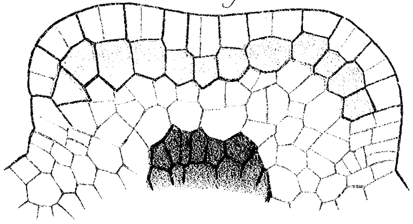
Fig. 76.



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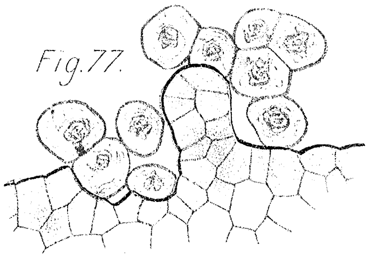


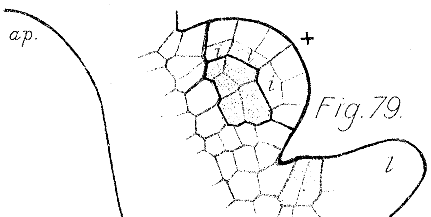
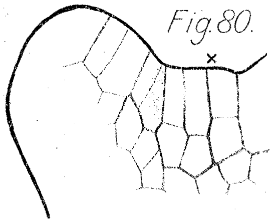


Fig. 79.

Fig. 80.



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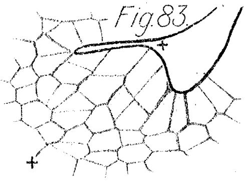

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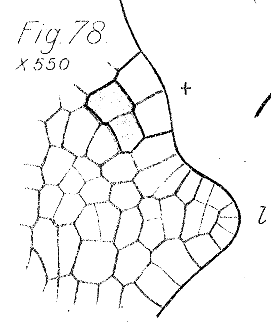

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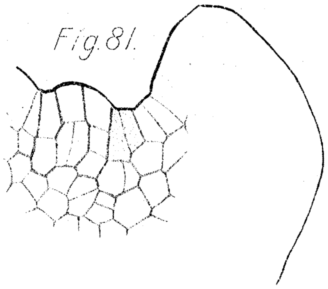

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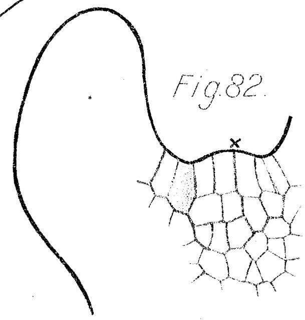
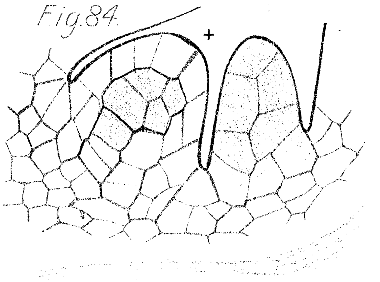


Fig. 84.



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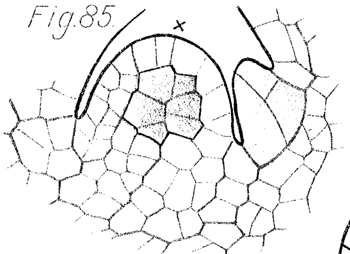

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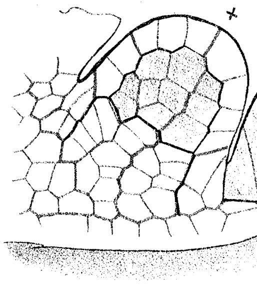


Fig. 88.

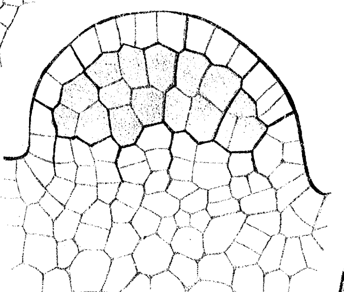


Fig. 87

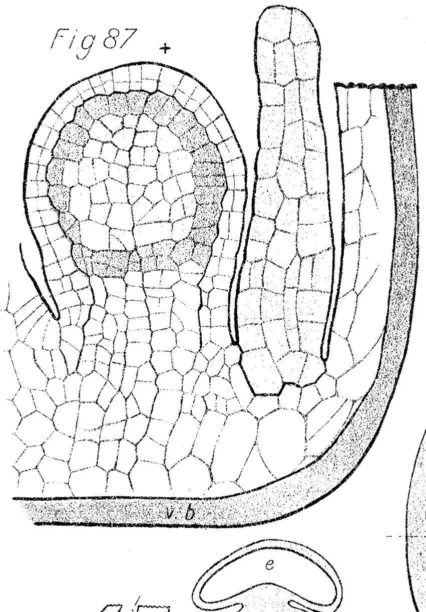
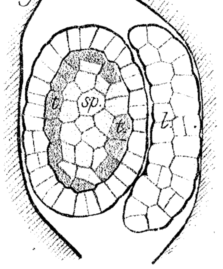


Fig. 89.



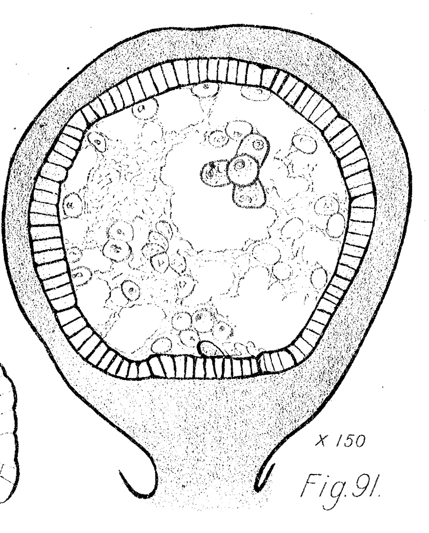


Fig. 91.

Fig. 90.

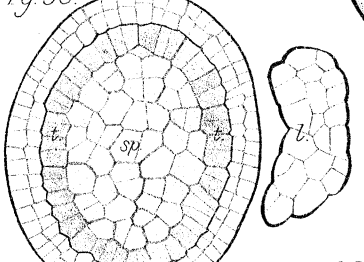
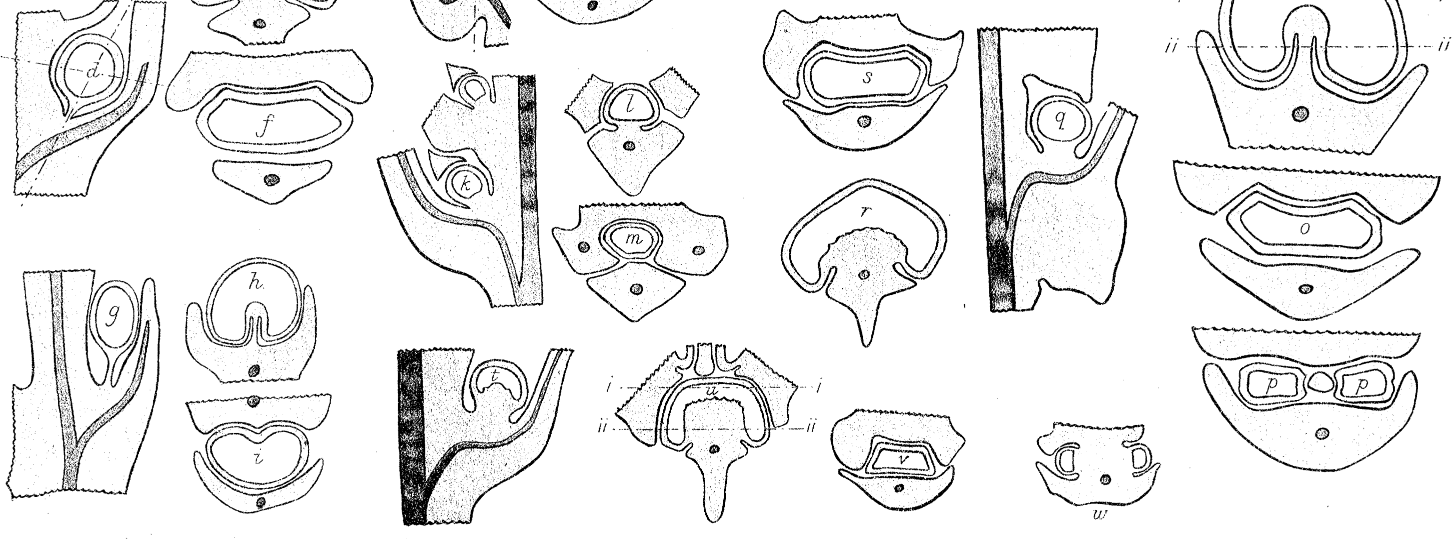


Fig. 92. a–w.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u
v
w
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i
ii
ii

Figs. 76–77. LYCOPODIUM ALPINUM. L.
Figs. 78–79. SELAGINELLA MARTENSII. SPRING.
Figs. 80–91. ,, SPINOSA. P.B.

Fig. 92. a–w OUTLINES OF SPORANGIA OF VARIOUS SPECIES.
a–c = PHYLLOGLOSSUM DRUMMONDII.
d–f = LYC. SELAGO.
g–i = LYC. PHLEGMARIA.
k–m = LYC. INUNDATUM.
n–p = LYC. CARINATUM.
q–s = LYC. ALPINUM.
t–w = LYC. CLAVATUM.

Bower del.

Fig. 93.

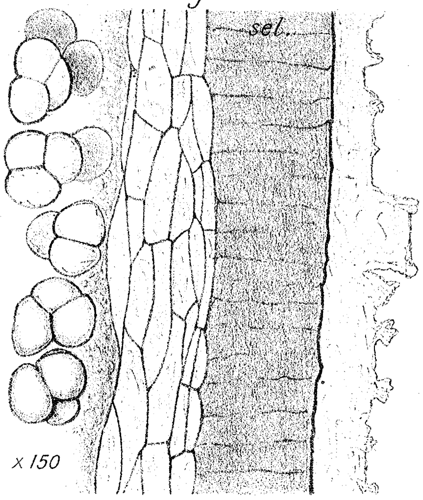


Fig. 94.

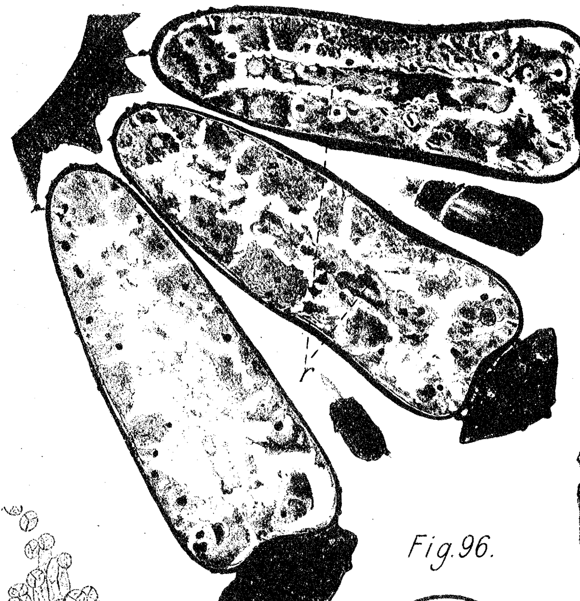


Fig. 95.

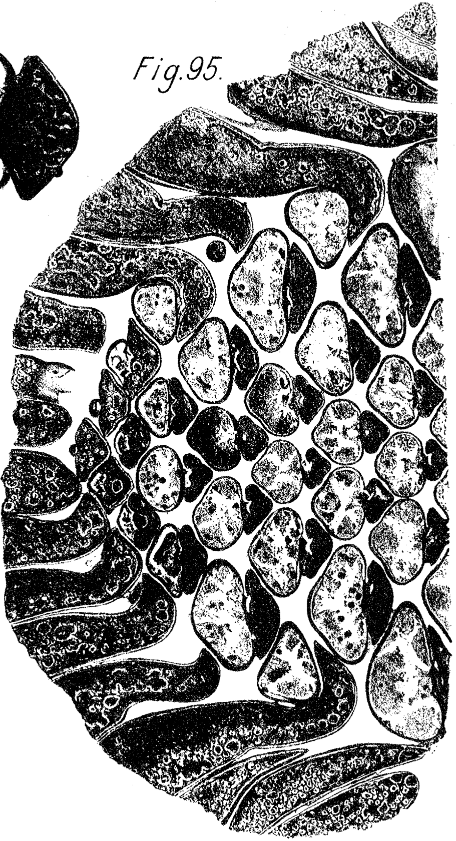
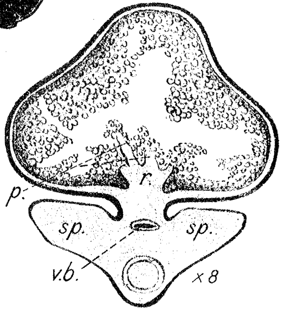


Fig. 96.


p.
r.
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v.b.
x 8

Fig. 97.

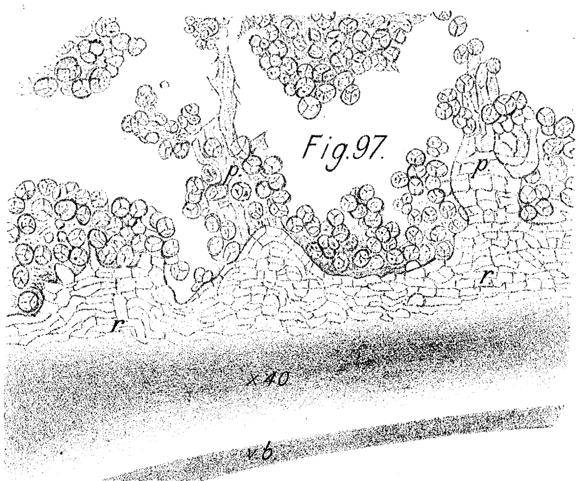


Fig. 99.

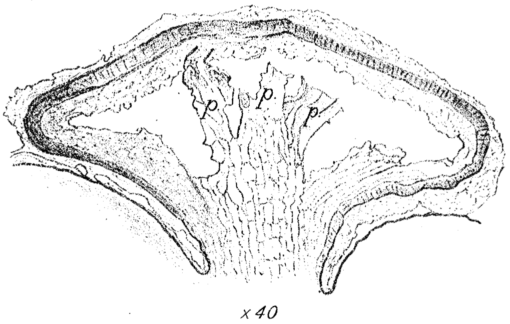


Fig. 100.

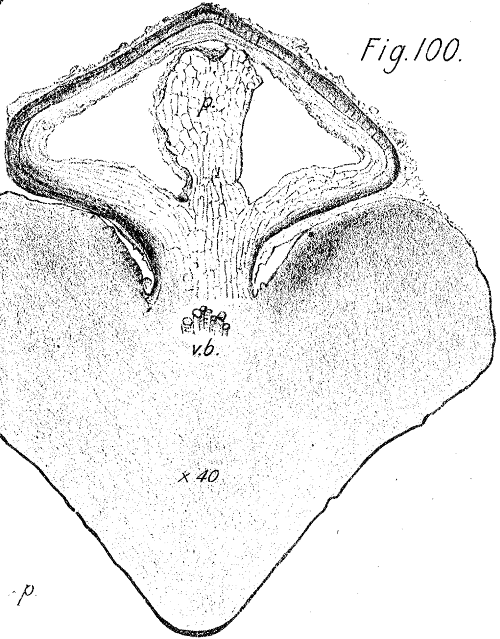
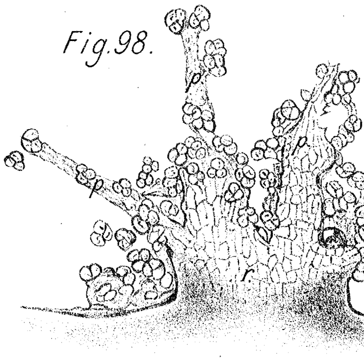


Fig. 98.



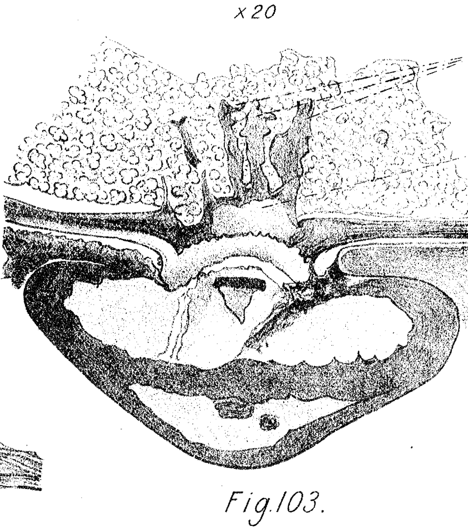
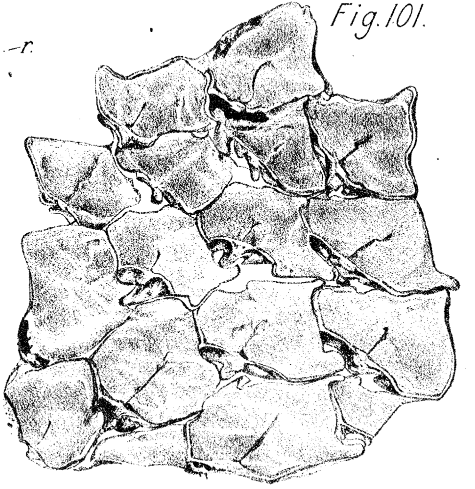


Fig. 103.

Fig. 101.



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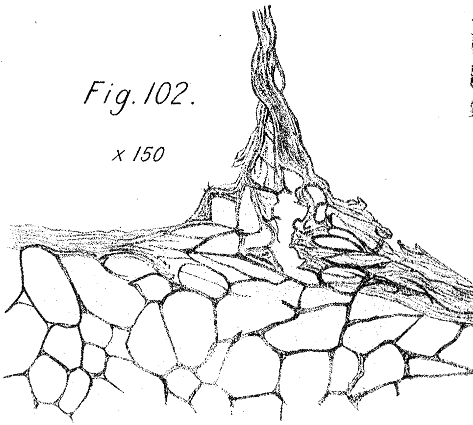


Fig^{s} 93-100. LEPIDODENDRON BROWNII. SCHPR.
Fig^{s} 101-102. LEPIDODENDRON SP. HOUGH HILL.
Fig. 103. LEPIDODENDRON BROWNII.

Bower del.
CAMBRIDGE ENGRAVING CO

Fig. 104.

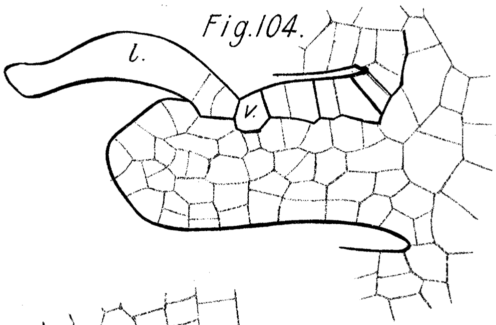


Fig. 105.

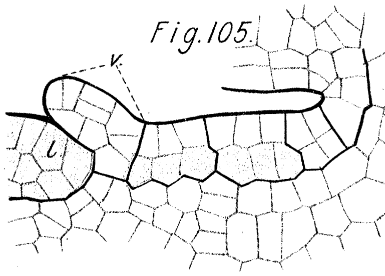


Fig. 106.

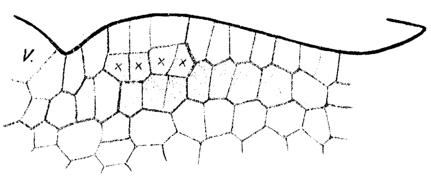


Fig. 107.

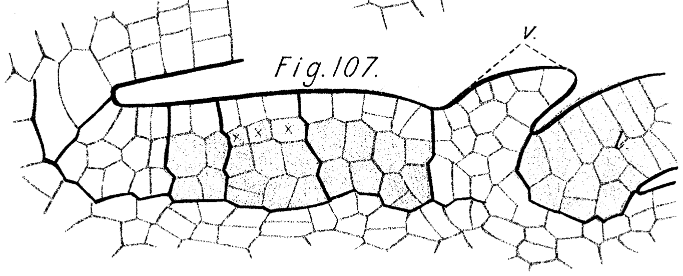


Fig. 108.

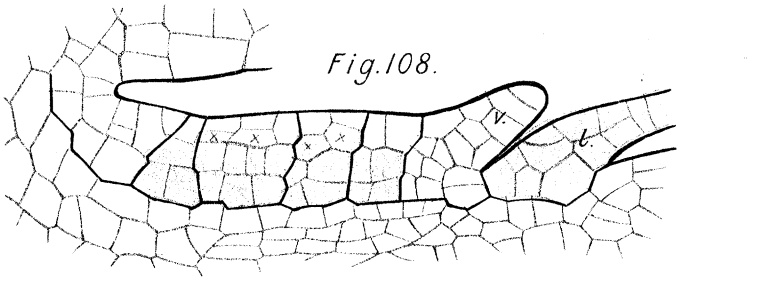


Fig. 109.

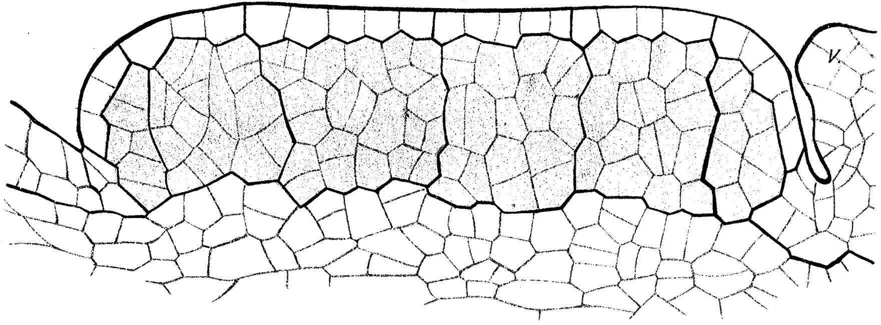
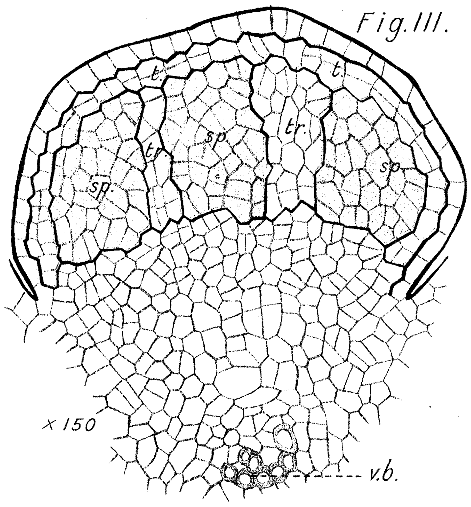


Fig. 111.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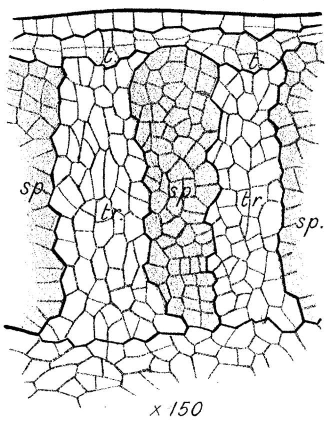
× 150
v.b.

Fig. 110.


*
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× 150

Fig. 113.

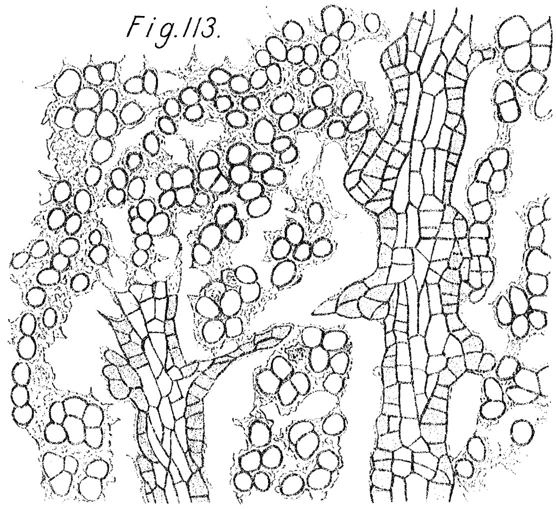


Fig. 112.

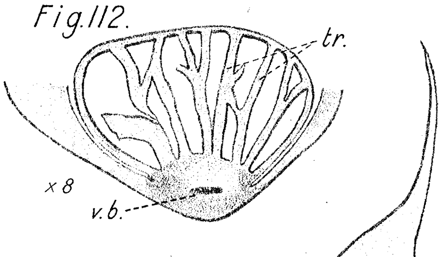


Fig. 116.

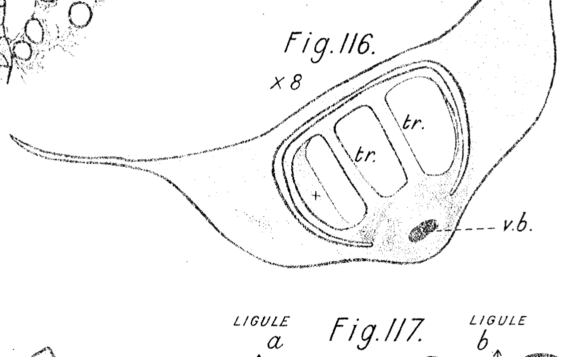
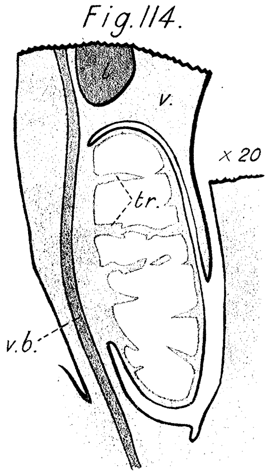


Fig. 114.



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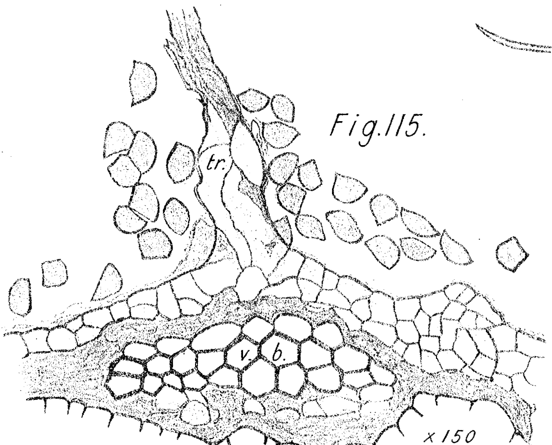
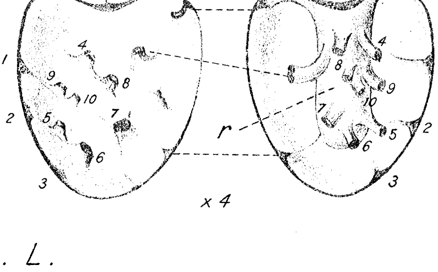


Fig. 117.


LIGULE a
LIGULE b
1
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Figs 104–117. ISOETES LACUSTRIS. L.

Bower del.
CAMBRIDGE ENGRAVING CO.

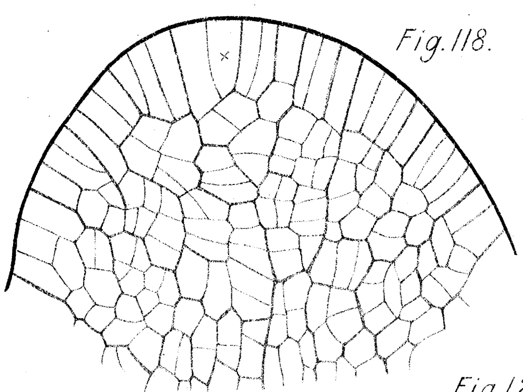

Fig. 118.

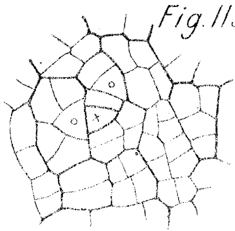

Fig. 119.

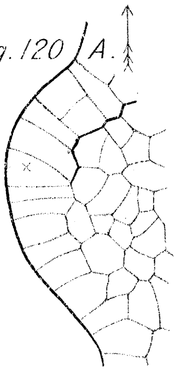

Fig. 120 A.

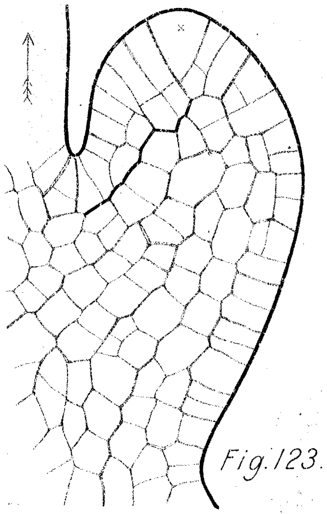

Fig. 123.

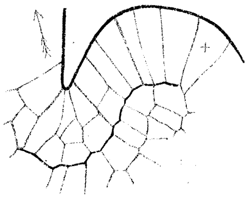

Fig. 120.

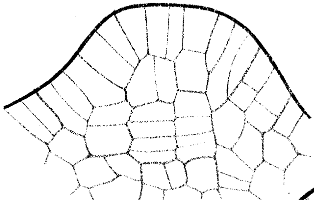

Fig. 122.

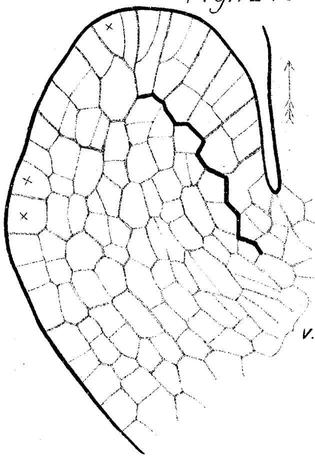

Fig. 124.

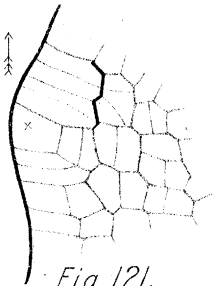

Fig. 121.

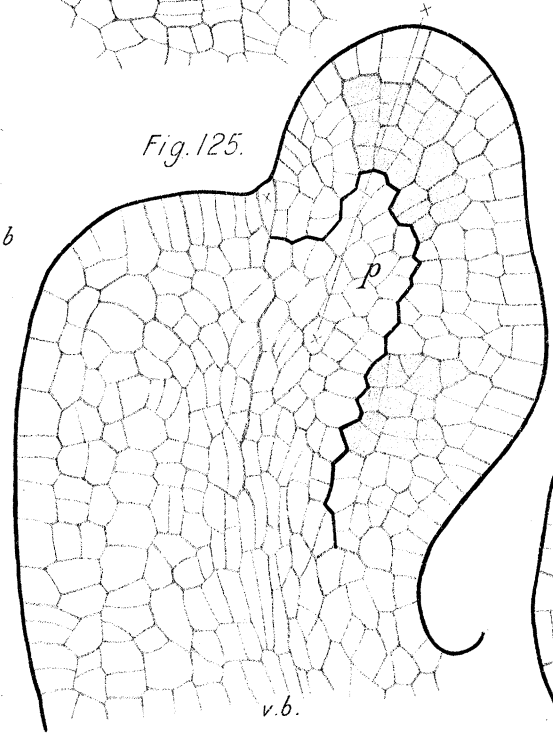

Fig. 125.

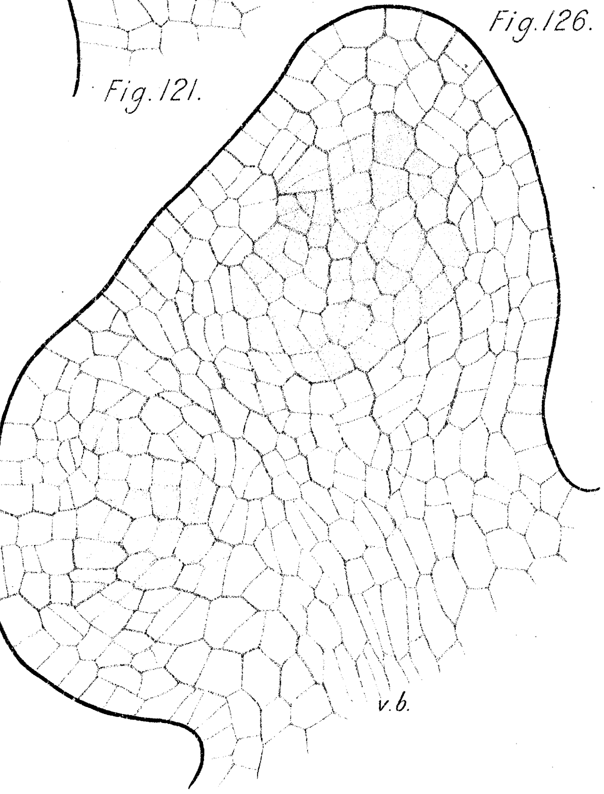

Fig. 126.

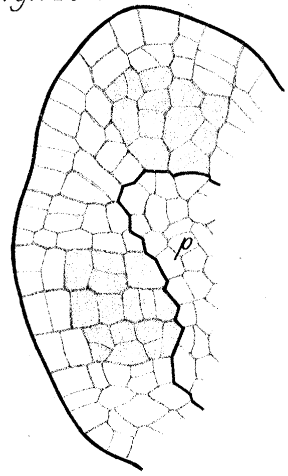

Fig. 125 bis.

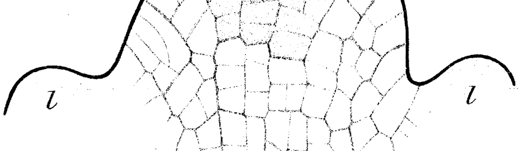

Fig. 127.

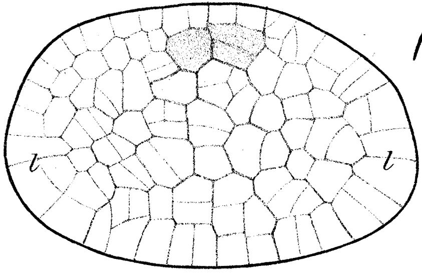

Fig. 129.

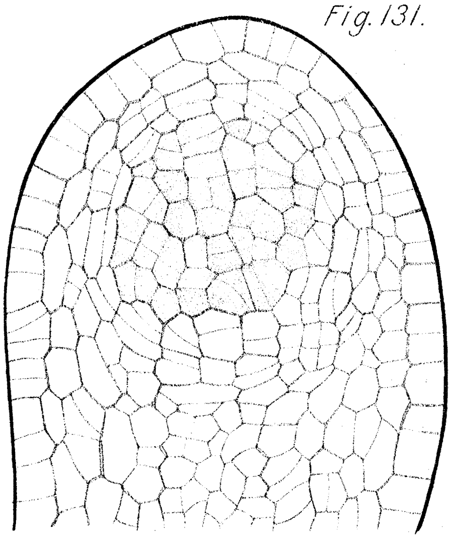

Fig. 131.

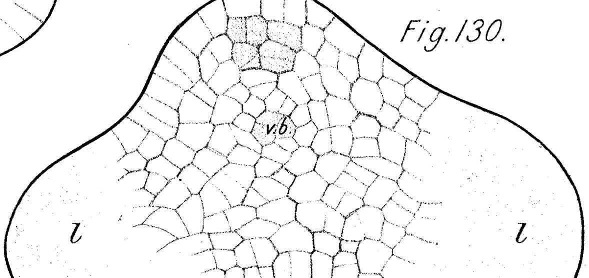

Fig. 130.

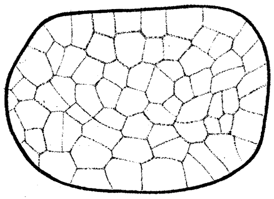

Fig. 128.

Figs 118 - 131. Tmesipteris tannensis Bernh.

Bower del.

CAMBRIDGE ENGRAVING CO.

Fig. 132.

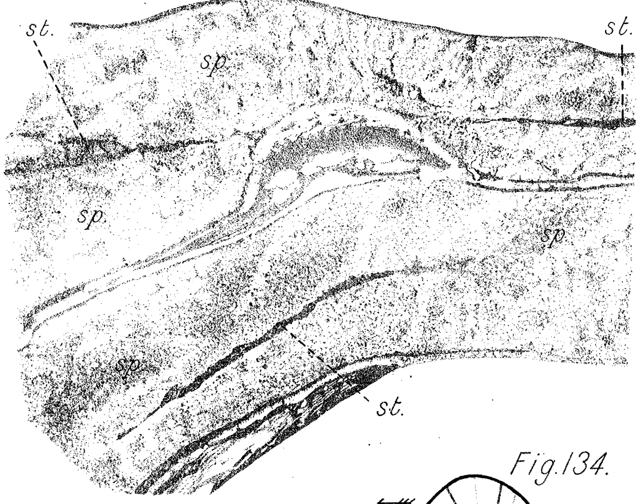
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Fig. 131. bis.

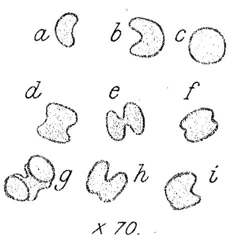
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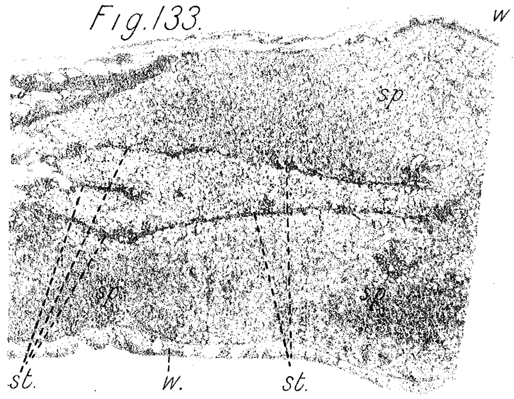
Fig. 133.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st.

Fig. 135.

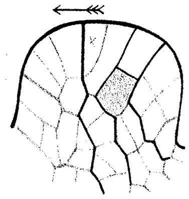


Fig. 134.

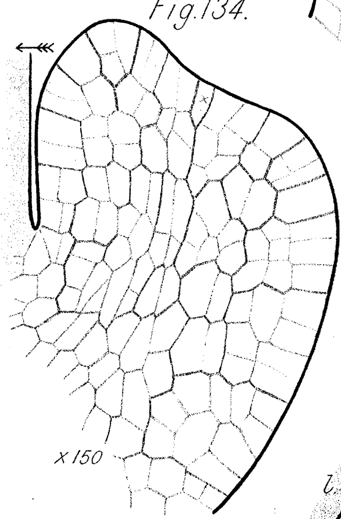
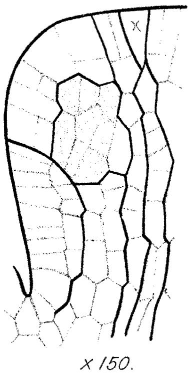


Fig. 136.



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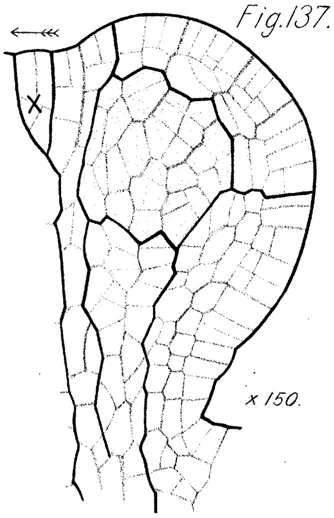

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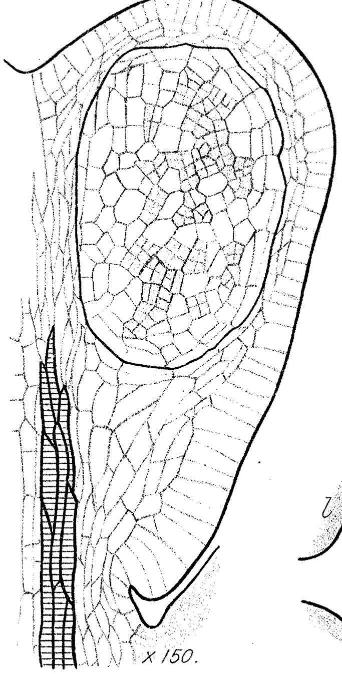

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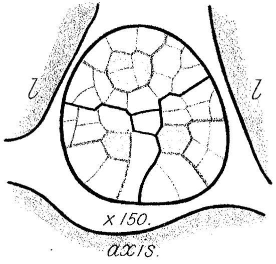
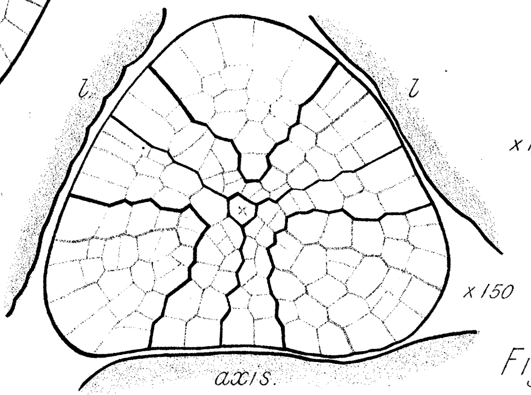

l
l
x 150.
axis.

Fig. 140.


l
l
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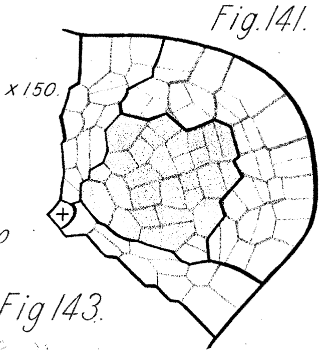
axis.

Fig. 141.



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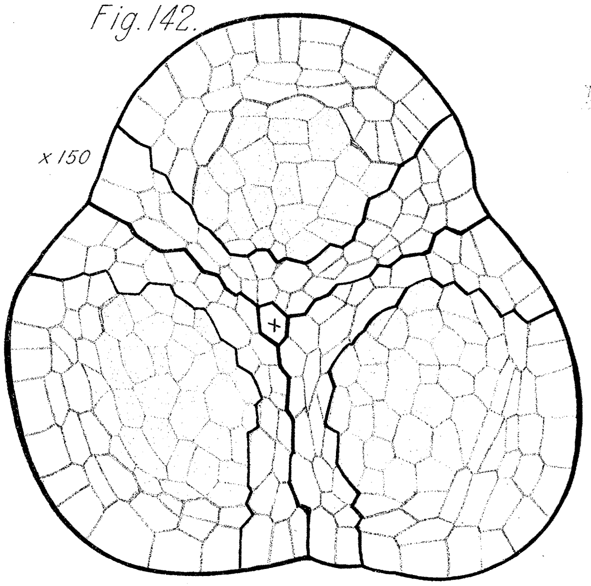

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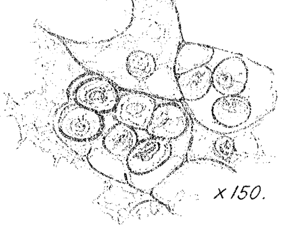

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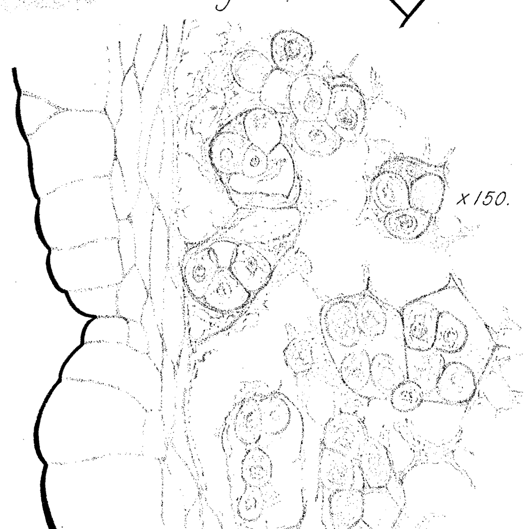
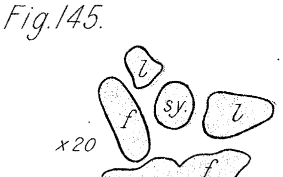


Fig. 145.


x 20
l
sy.
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f
f
ax.
l
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sy.
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l

Figs. 132. 133. LEPIDODENDRON.

Figs. 135–144. PSILOTUM TRIQUETRUM. SW.

Fig. 145. TMESIPTERIS TANNENSIS. BERNH.

Bower del.

CAMBRIDGE ENGRAVING CO.

Fig. 146.

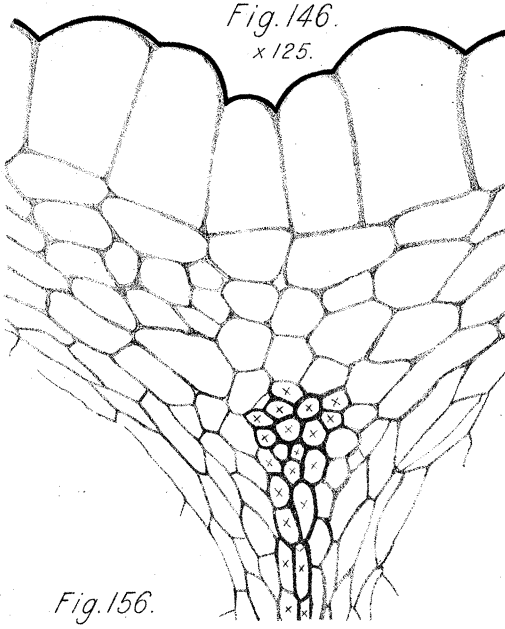


Fig. 147.

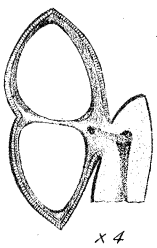


Fig. 148.

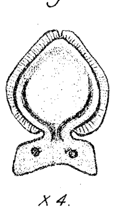
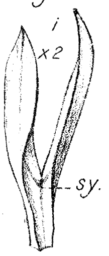


Fig. 149.



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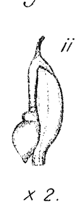

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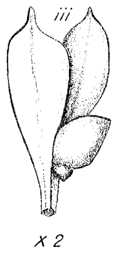
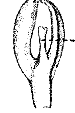


Fig. 152.



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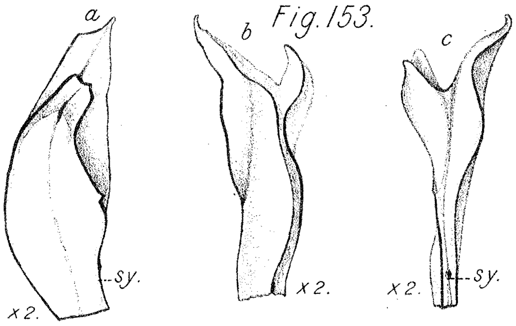
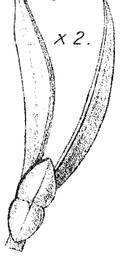

a
b
c
sy.
x 2.
x 2.
x 2.
sy.

lateral abaxial adaxial.

Fig. 154.



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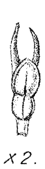

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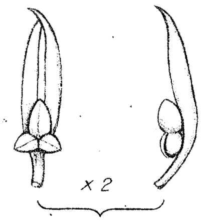

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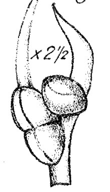


Fig. 158.

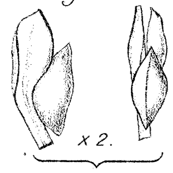
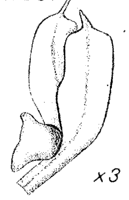


Fig. 159.



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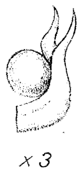

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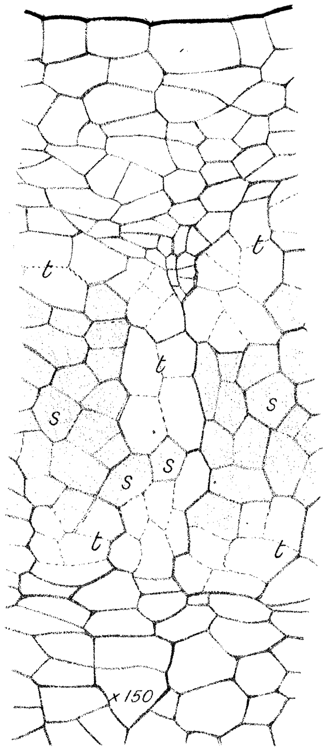
t
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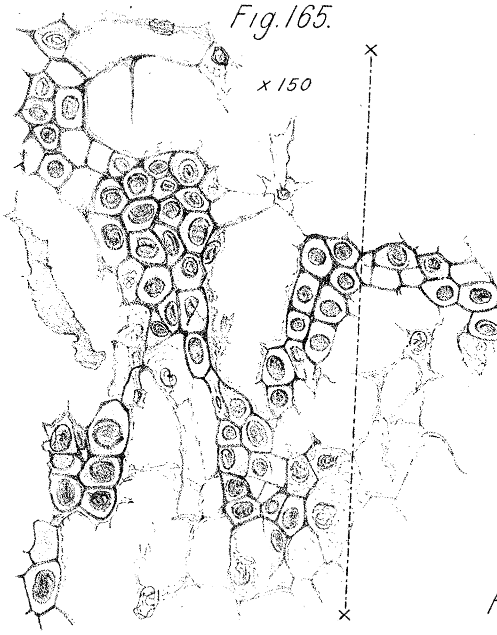
t
x 150

Fig. 165.



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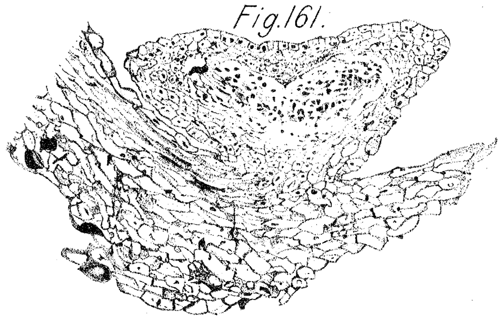

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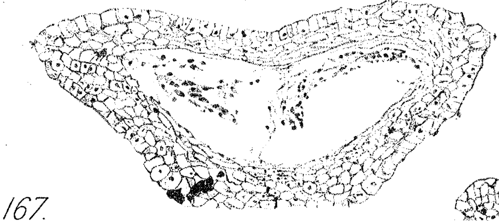


Fig. 164.

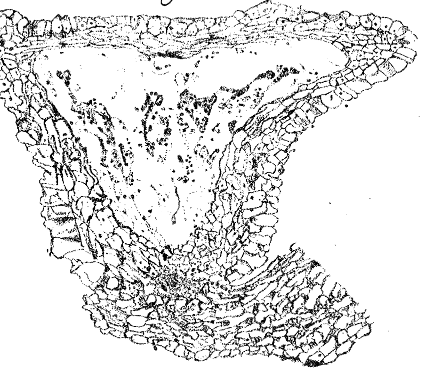


Fig. 166.

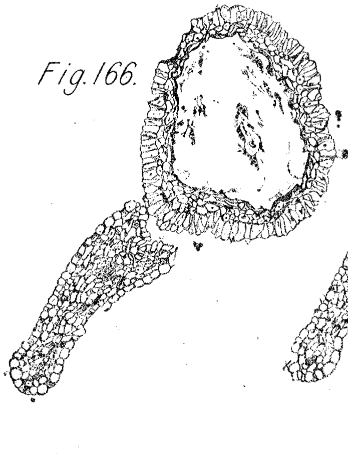


Fig. 167.

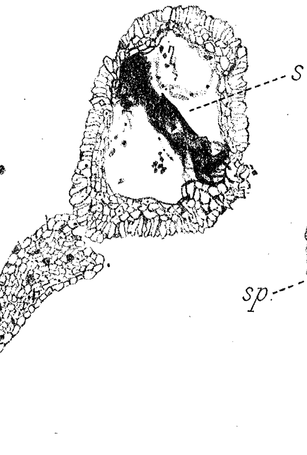
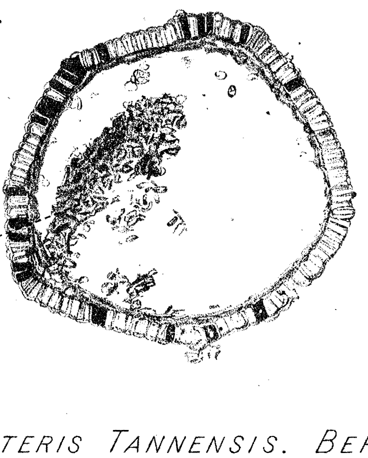


Fig. 168.



Figs 146–168. TMESIPTERIS TANNENSIS. BERNH.

Bower del.
CAMBRIDGE ENGRAVING CO.

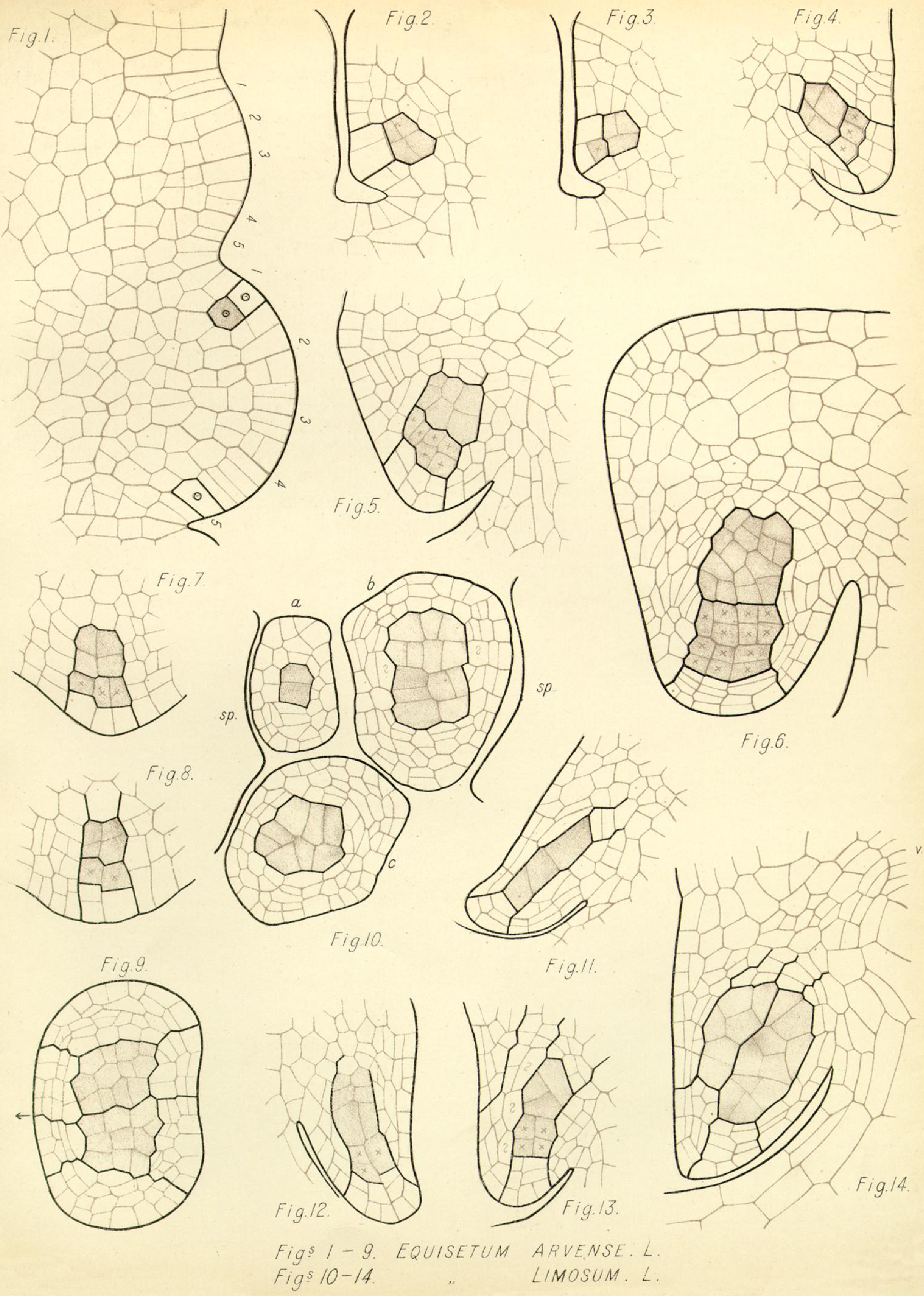


PLATE 42.

Equisetum arvense, L.

Fig. 1. Radial longitudinal section of part of a young strobilus, showing two sporangiophores in a very young state. (× 300.)

Fig. 2. Part of an older sporangiophore in radial section, with young sporangium: the group of cells shaded corresponds to the cell shaded in fig. 1. (× 300.)

Fig. 3. Ditto, showing the first periclinal division in the outer cell. (× 300.)

Fig. 4. Ditto; considerably older, and showing cells (×) which are added to the archesporium as the result of subdivision of the outer of the two original cells. (× 300.)

Fig. 5. Ditto; older. Cells marked (×) correspond to those in the previous figure. (× 300.)

Fig. 6. Ditto; a good deal older. All the essential parts of the sporangium are here initiated. (× 300.)

Fig. 7. Oblique section through a sporangiophore of age corresponding to fig. 4, so as to pass through the axis of the young sporangium in a plane at right angles to that of fig. 4. (× 300.)

Fig. 8. A section similar to fig. 7. (× 300.)

Fig. 9. Transverse section through a sporangium of age corresponding to that shown in fig. 6. (× 300.) The arrow indicates the side next to the stalk of the sporangiophore.

Equisetum limosum, L.

Fig. 10. Part of a tangential section of a strobilus, which traverses the sporangiophores transversely. *sp.* = stalks of sporangiophores. *a*, *b*, *c* = three sporangia cut transversely, and showing extreme differences of size and complexity in sporangia side by side. (× 300.)

Figs. 11, 12, 13. Three sporangia from the same strobilus, cut in median longitudinal section, and showing different types of segmentation, together with difference of bulk. (× 300.)

Fig. 14. Median section of a rather older sporangium, from near the apex of a strobilus. *v.b.* shows where the vascular bundle is beginning to be developed. (× 300.)

v.b Fig. 15.

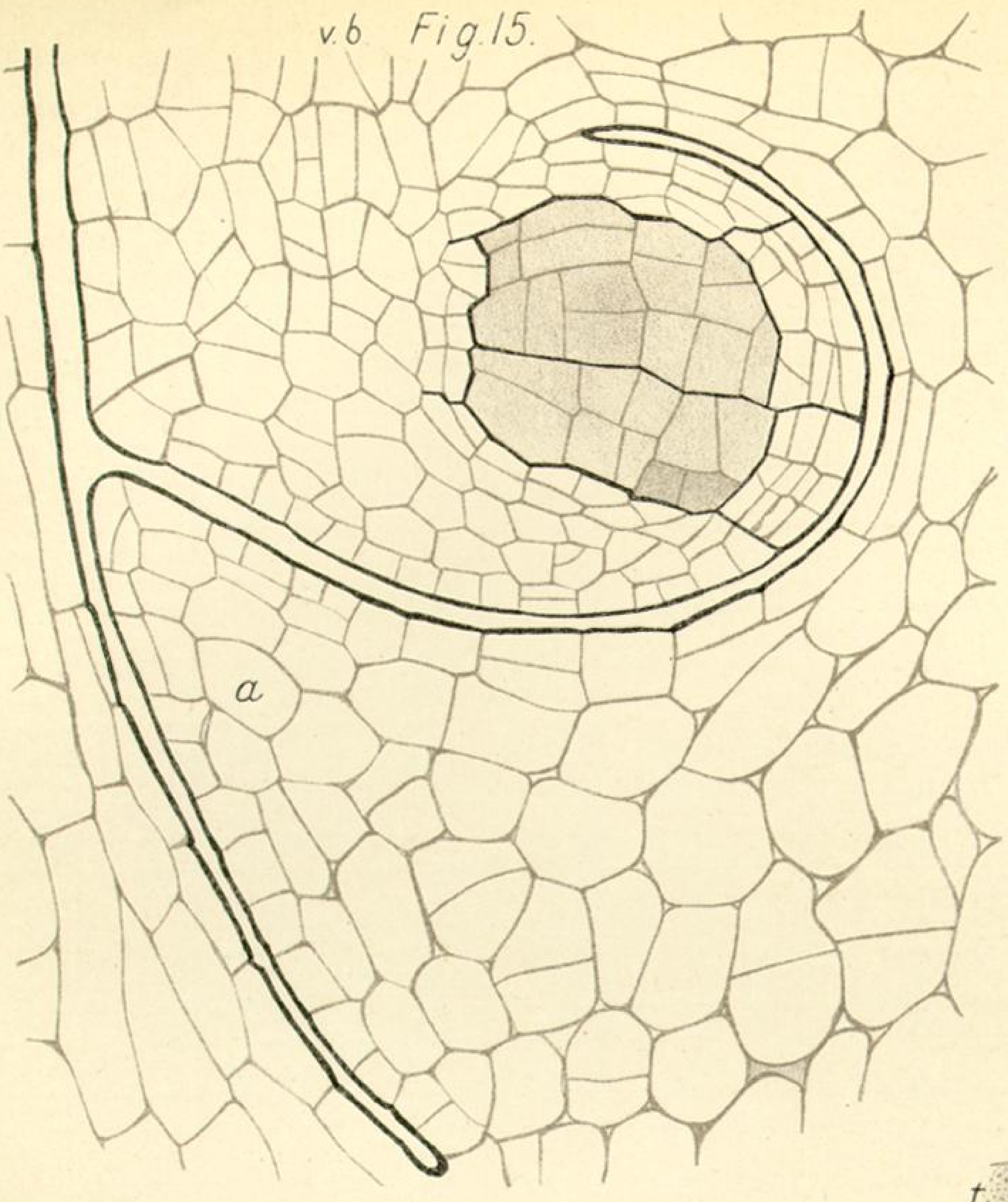


Fig. 16.

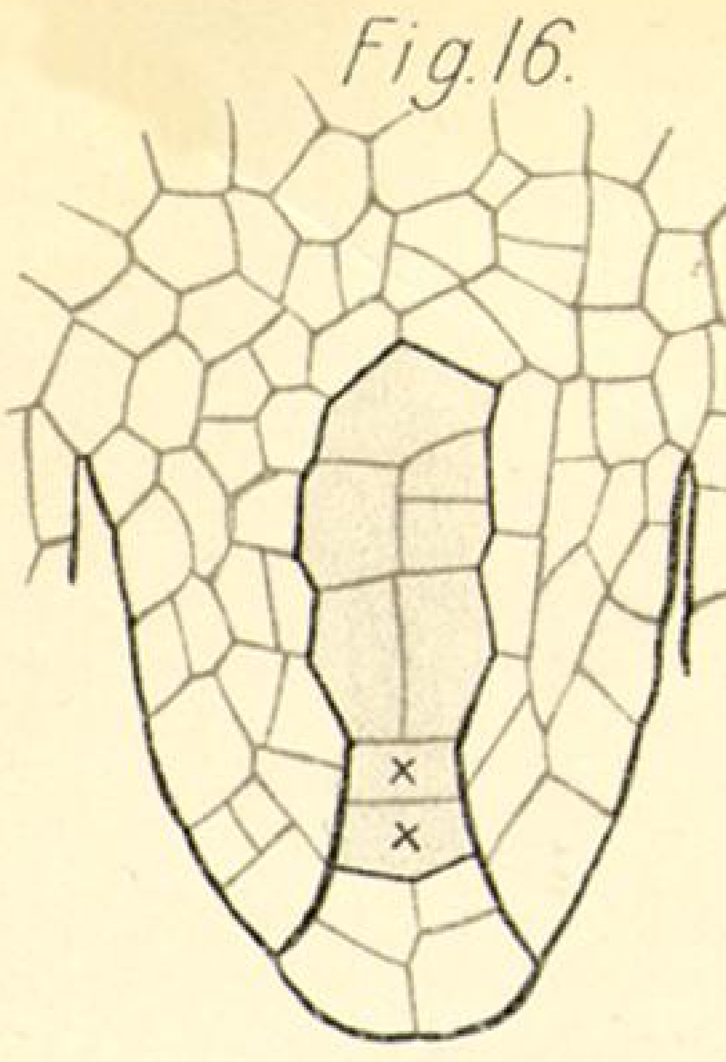


Fig. 17.

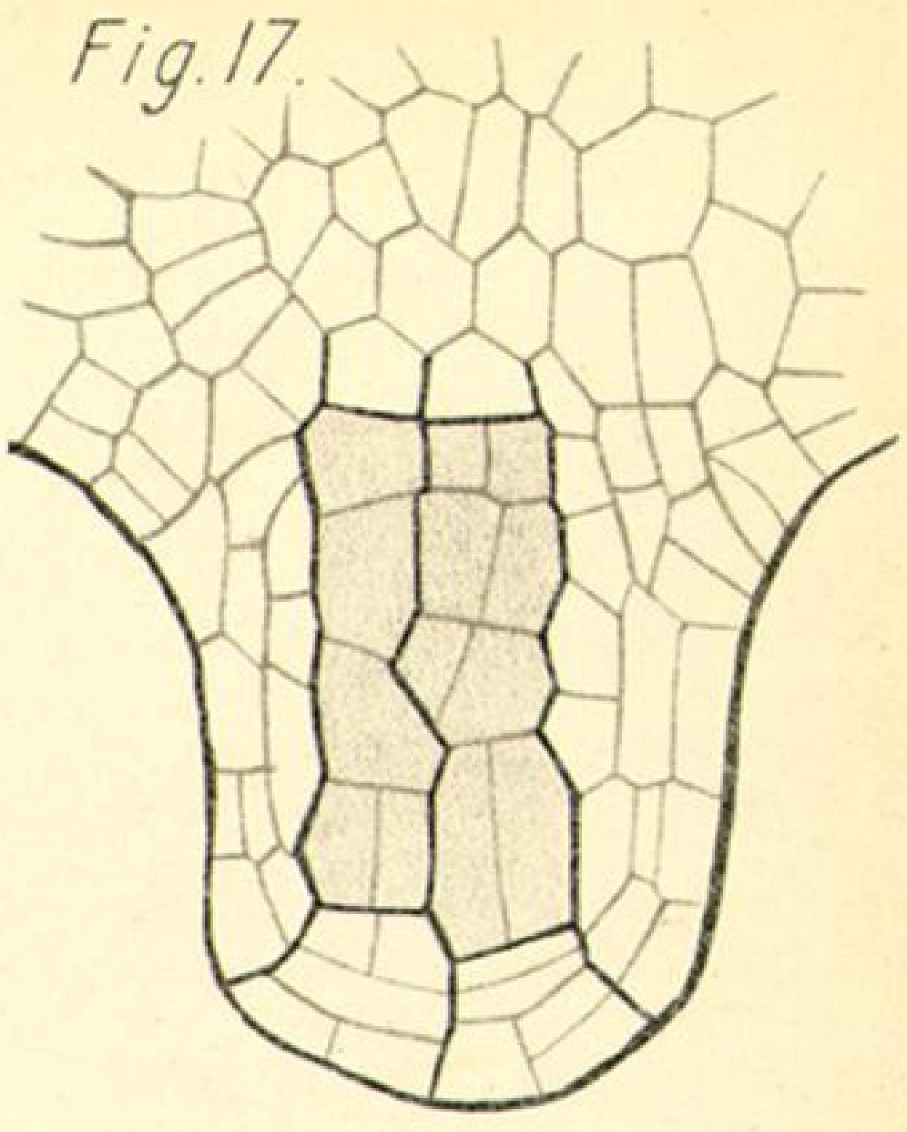


Fig. 18.

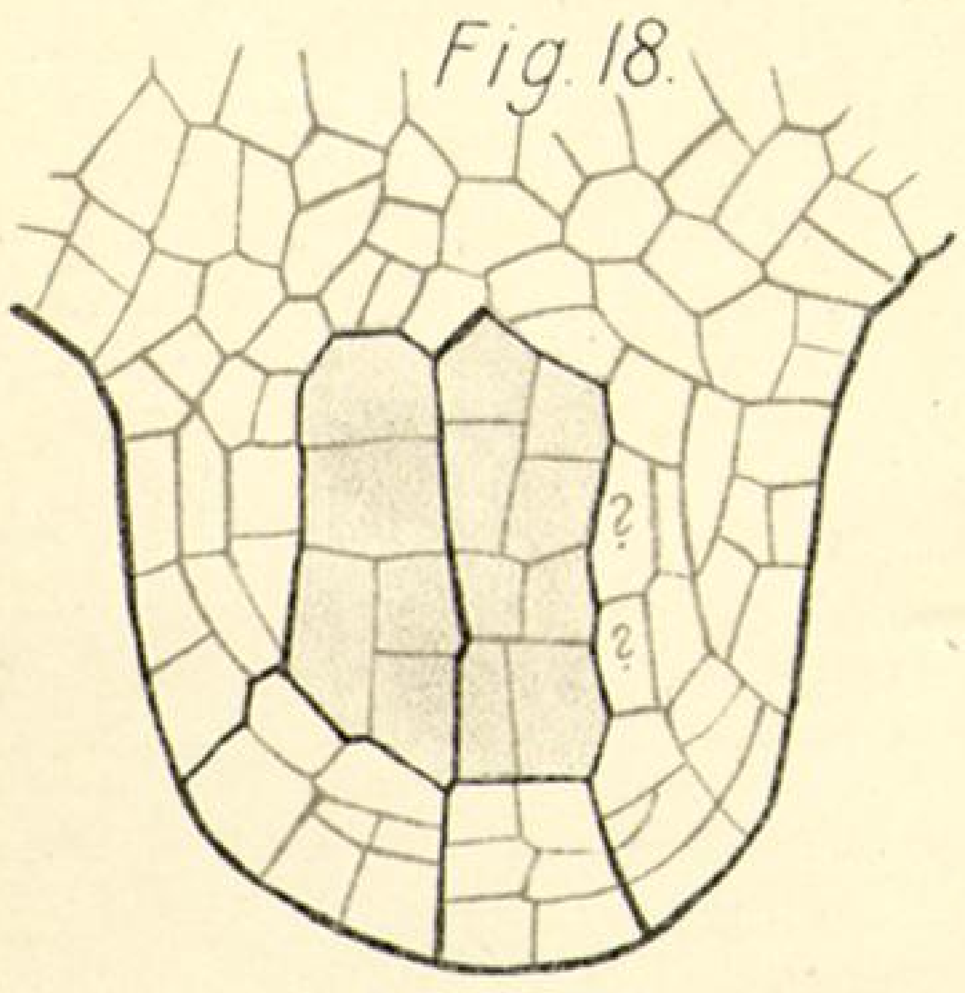


Fig. 19.

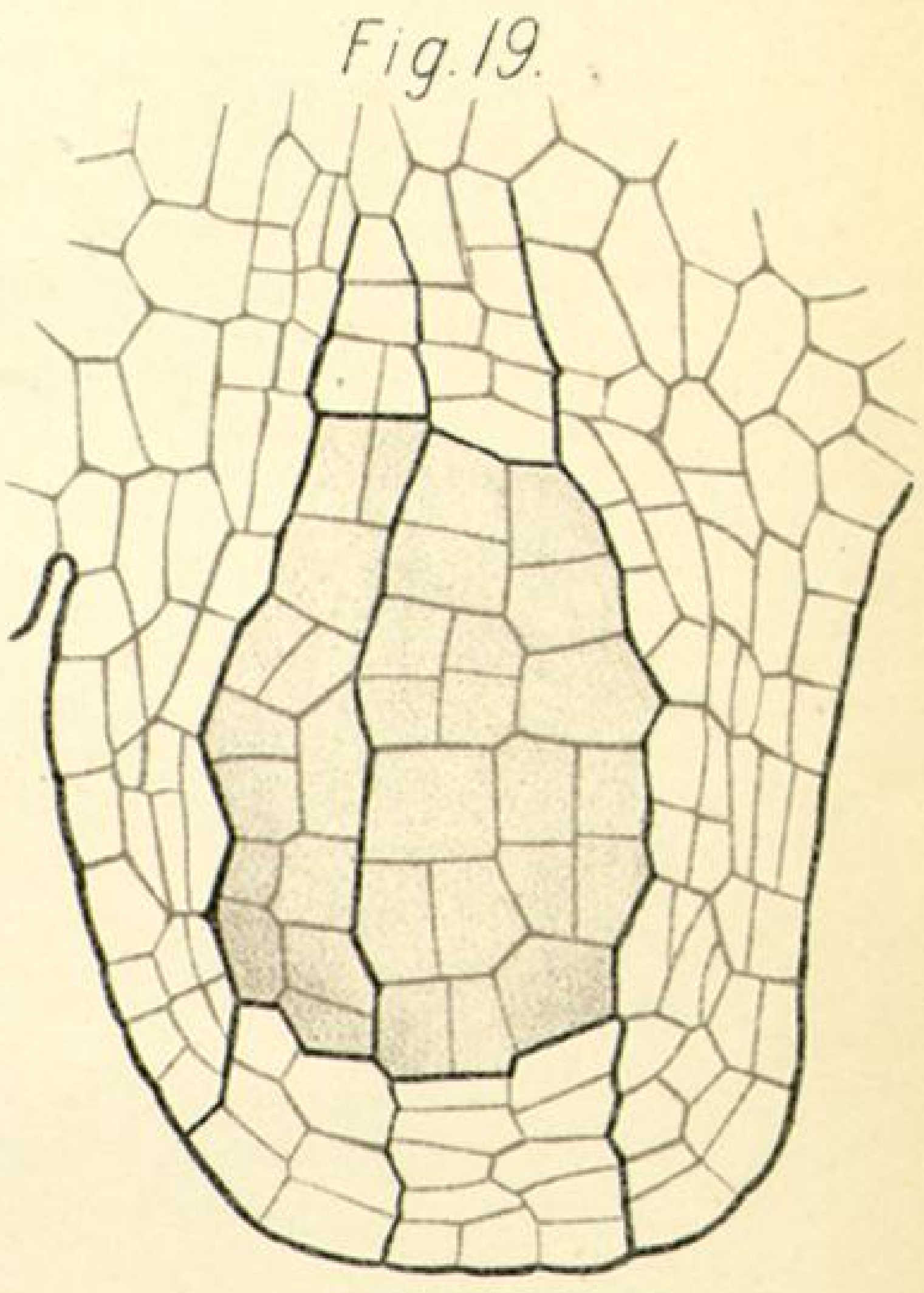


Fig. 20.

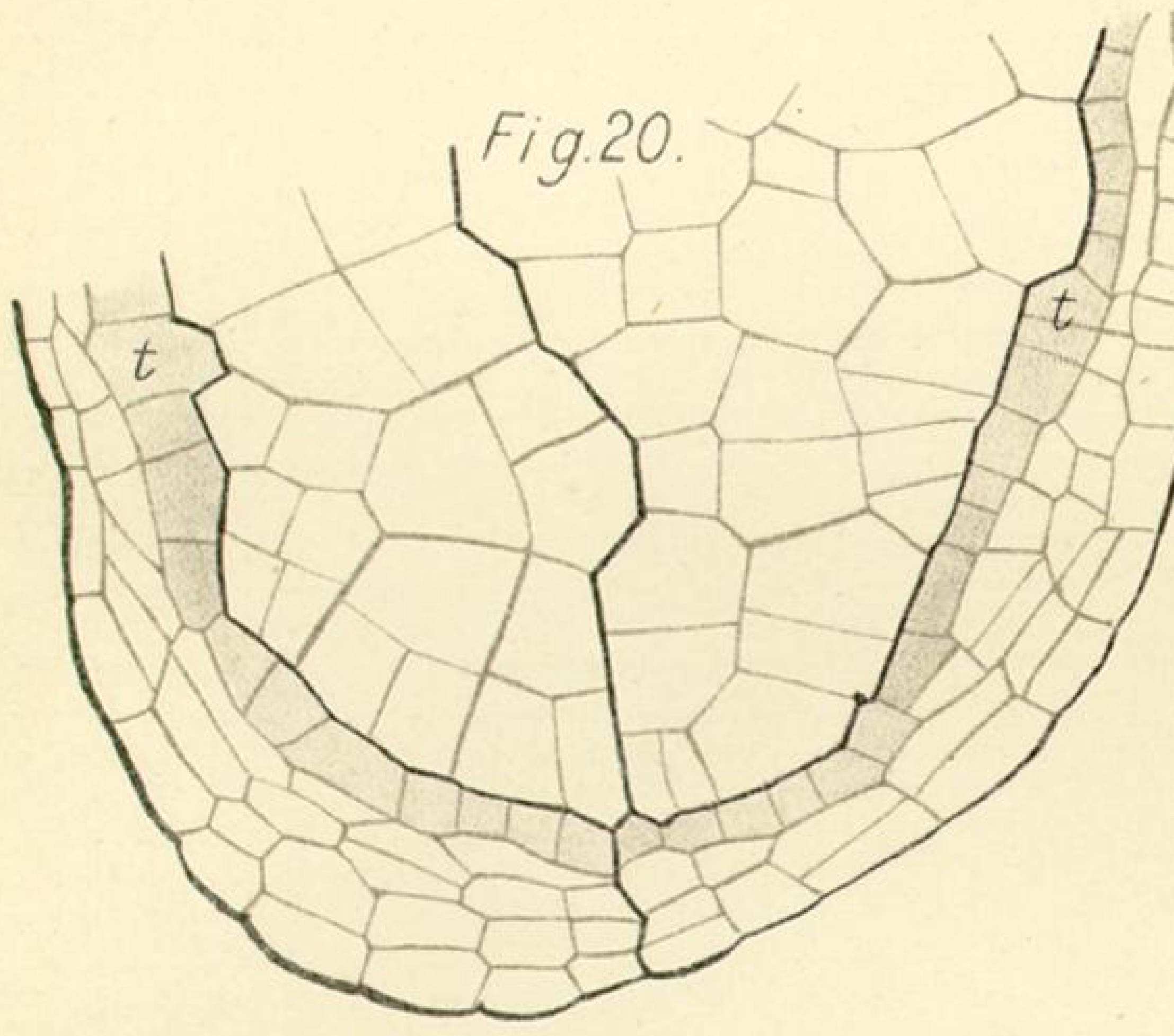


Fig. 21.

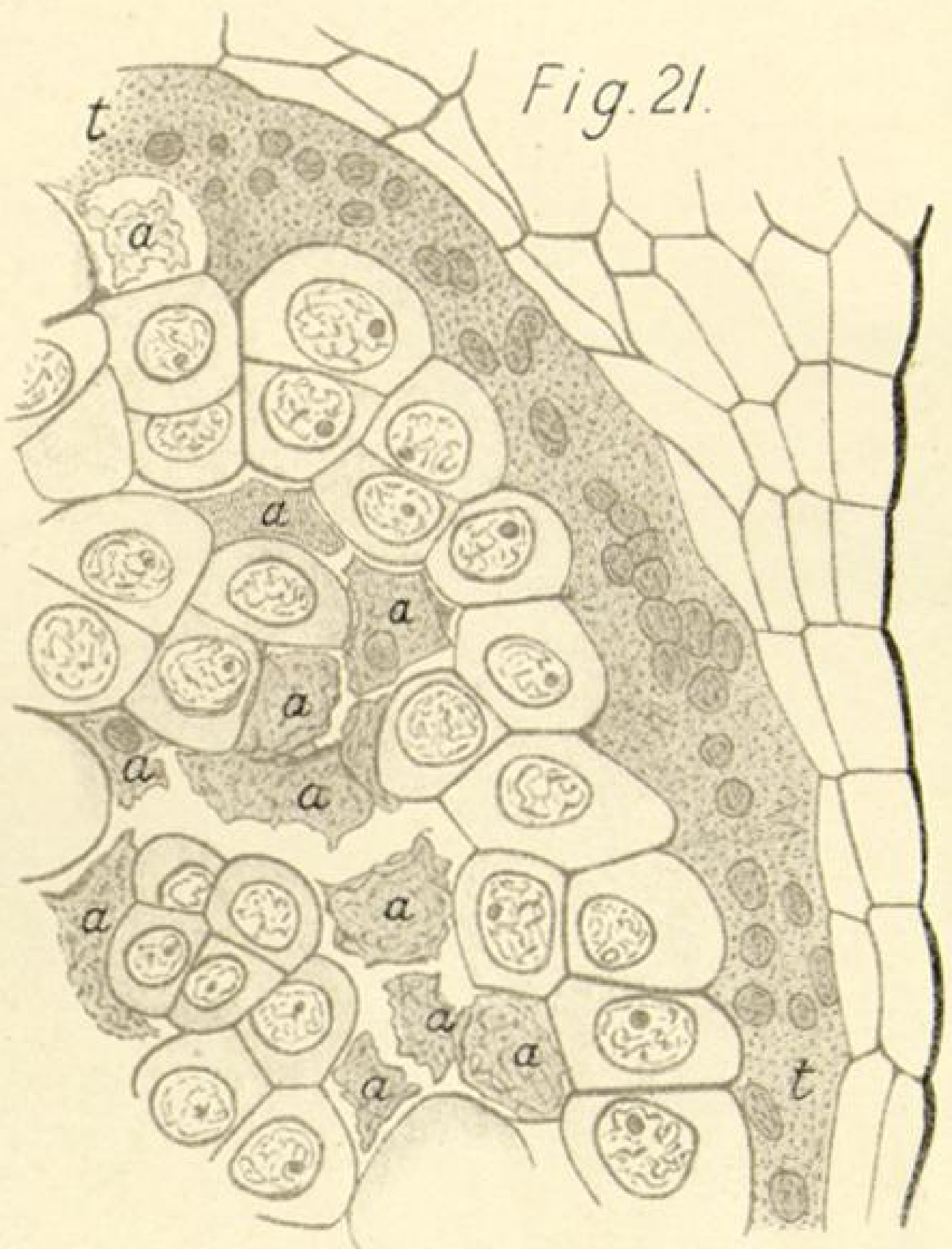


Fig. 24.

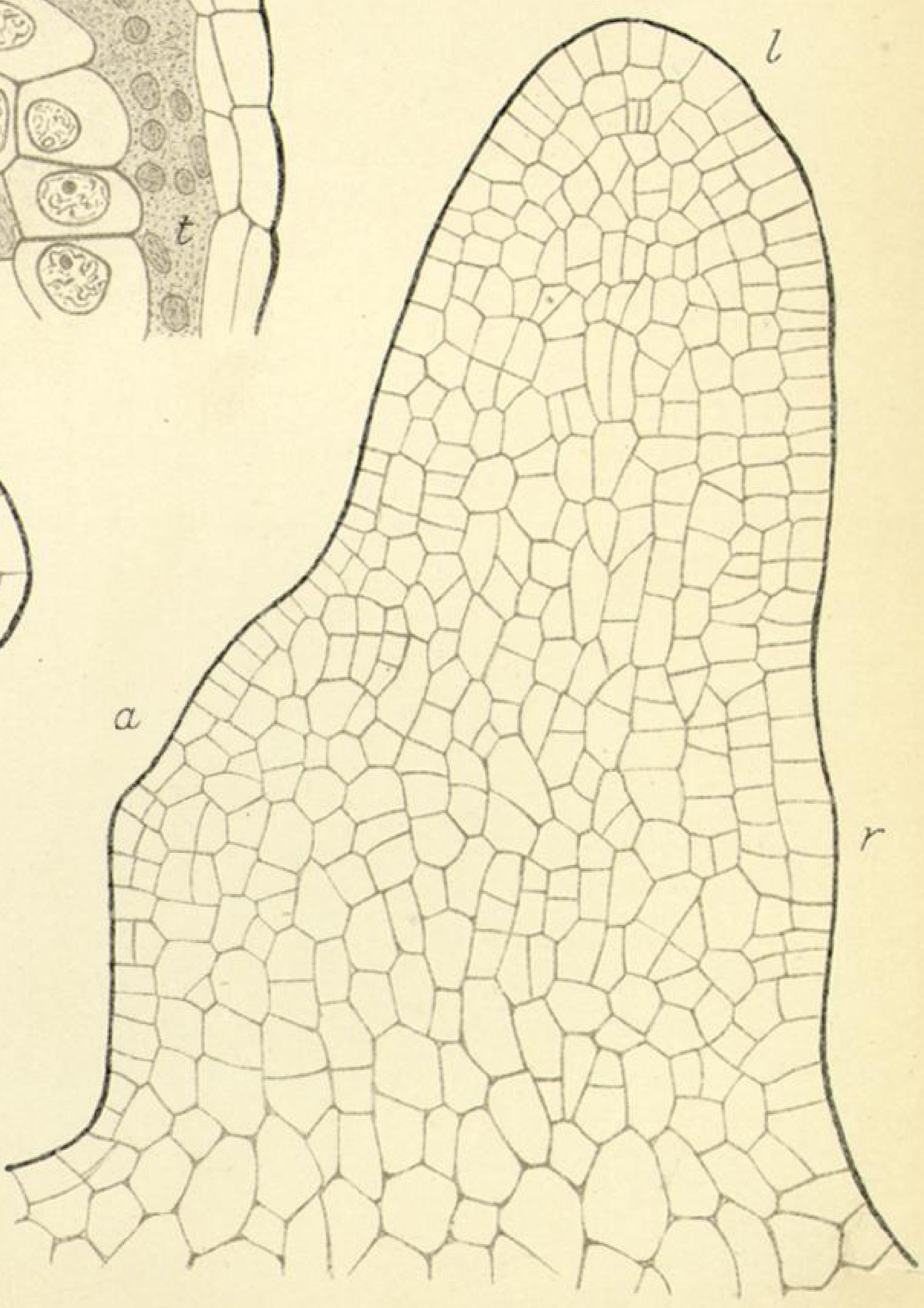


Fig. 22.

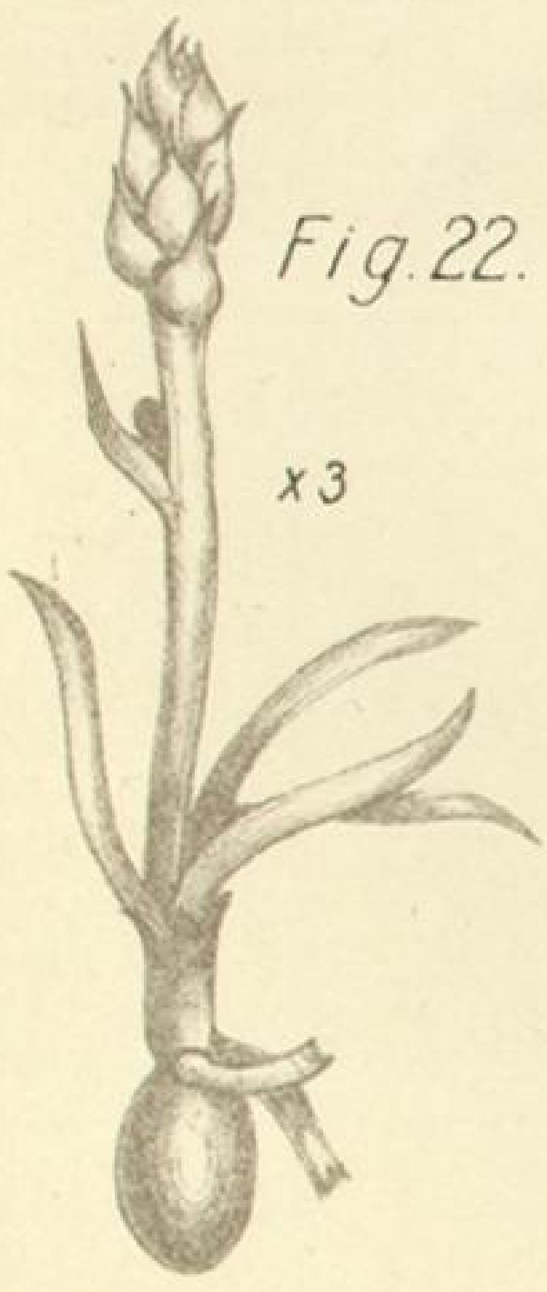


Fig. 23.

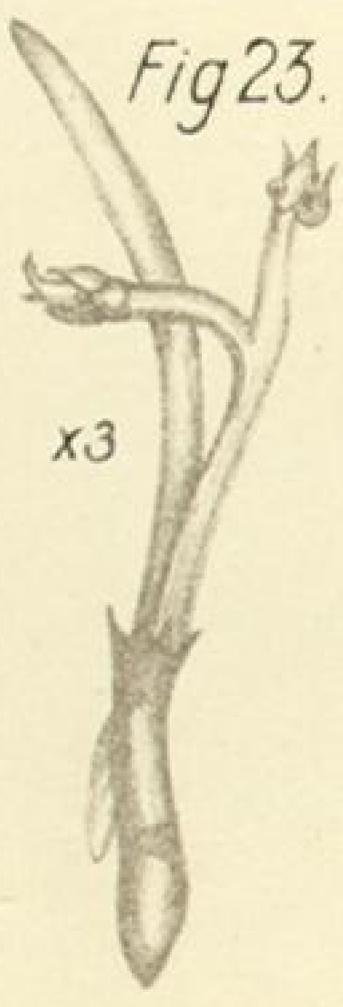
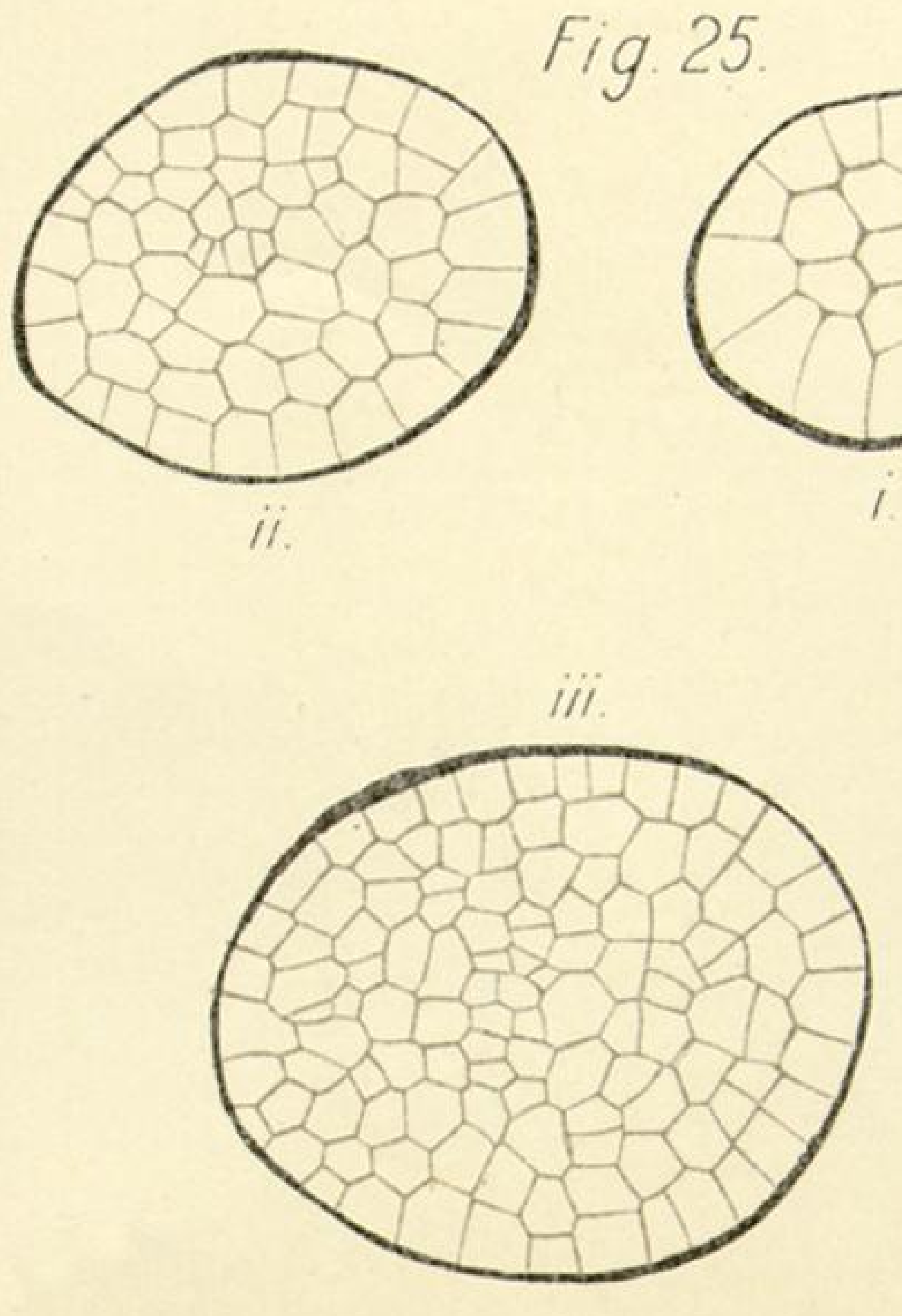


Fig. 25.



Figs 15-21. EQUISETUM LIMOSUM. L.
Figs 22-24. PHYLLOGLOSSUM DRUMMONDII. KUNZE.

PLATE 43.

Fig. 15. Median longitudinal section of a sporangium at the base of the strobilus, together with the annulus (*a.*). (× 300.)

Fig. 16. Tangential section of a sporangium of same age as figs. 11–13. (× 300.) Compare fig. 11.

Figs. 17, 18. Ditto; more complex specimens. (× 300.)

Fig. 19. Tangential section of a sporangium in a more advanced state. (× 300.)

Fig. 20. Apex of an older sporangium in radial section. The tapetum (*t*) is now clearly defined. (× 300.)

Fig. 21. Part of an older sporangium, showing the tapetum (*t.*) still a clearly-defined band, though the individuality of the cells is lost; within this the sporogenous tissue, of which certain cells (*a*) are abortive. (× 300.)

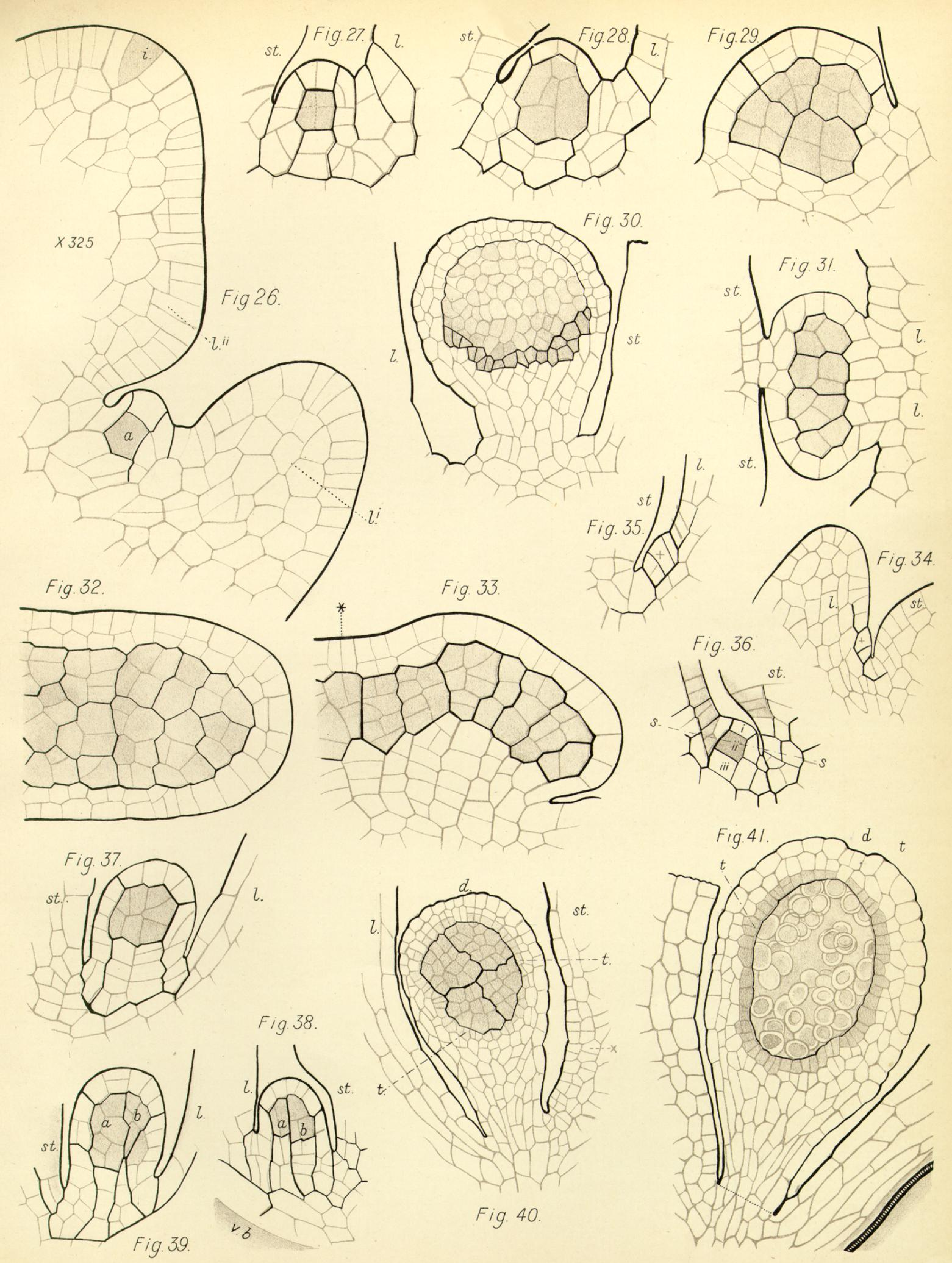
Phylloglossum Drummondii, Kunze.

Fig. 22. A plant of *Phylloglossum*, showing tuber-leaves and strobilus; one sporophyll of the latter is at a distance below the rest, intercalary growth having taken place in the axis above it. (× 3.)

Fig. 23. A plant of *Phylloglossum* grown in the Glasgow Botanic Garden; the strobilus is branched into two unequal parts. (× 3.)

Fig. 24. Median longitudinal section through the plant represented as fig. 8 in 'Phil. Trans.,' 1885, Plate 71. *a.* = apex; *l.* = leaf (protophyll); *r.* = root (× 150.)

Fig. 25 (i., ii., iii.) Successive transverse sections of the young leaf (protophyll) of the plant represented as fig. 10 in 'Phil. Trans.,' 1885, Plate 71. (× 150.)



Figs 26-33. PHYLLOGLOSSUM DRUMMONDII. KUNZE.
Figs 34-41. LYCOPODIUM SELAGO. L.

PLATE 44.

Fig. 26. Apex of a strobilus in median longitudinal section showing an initial cell (*i*), two sporophylls (*l′ l″*), the latter just beginning to be developed; in connection with *l′* is a sporangium, of which the archesporium (*a*) consists apparently of one cell. (× 325.)

Fig. 27. Another section from the same sporangium, showing further segmentations, which may have been present in the section shown in fig. 26, but made invisible by the method of clearing used. (× 325.)

Fig. 28. A slightly older sporangium in radial section. (× 325.)

Fig. 29. An older sporangium, in which periclinal divisions have begun in the cells of the wall of the sporangium. (× 325.)

Fig. 30. Radial section of a sporangium, in which the sporogenous cells are beginning to separate, but the tapetum is not yet formed from the inner layer of the wall. (× 150.)

Fig. 31. Transverse section of a young sporangium. (× 300.)

Fig. 32. Transverse section of a sporangium, of which one-half is shown; the stage is slightly younger than that of fig 30. (× 300.)

Fig. 33. Tangential section of a sporangium, of which rather more than one half is shown; the asterisk indicates the middle of the sporangium. (× 325.)

Lycopodium Selago, L.

Fig. 34. Radial section through a sporophyll (*l*) at the base of which a sporangium is beginning to make its appearance as a slight swelling. (× 300.)

Fig. 35. A similar sporangium, in radial section, rather more advanced. (× 300.)

Fig. 36. Ditto, older; the archesporium is shaded. (× 300.)

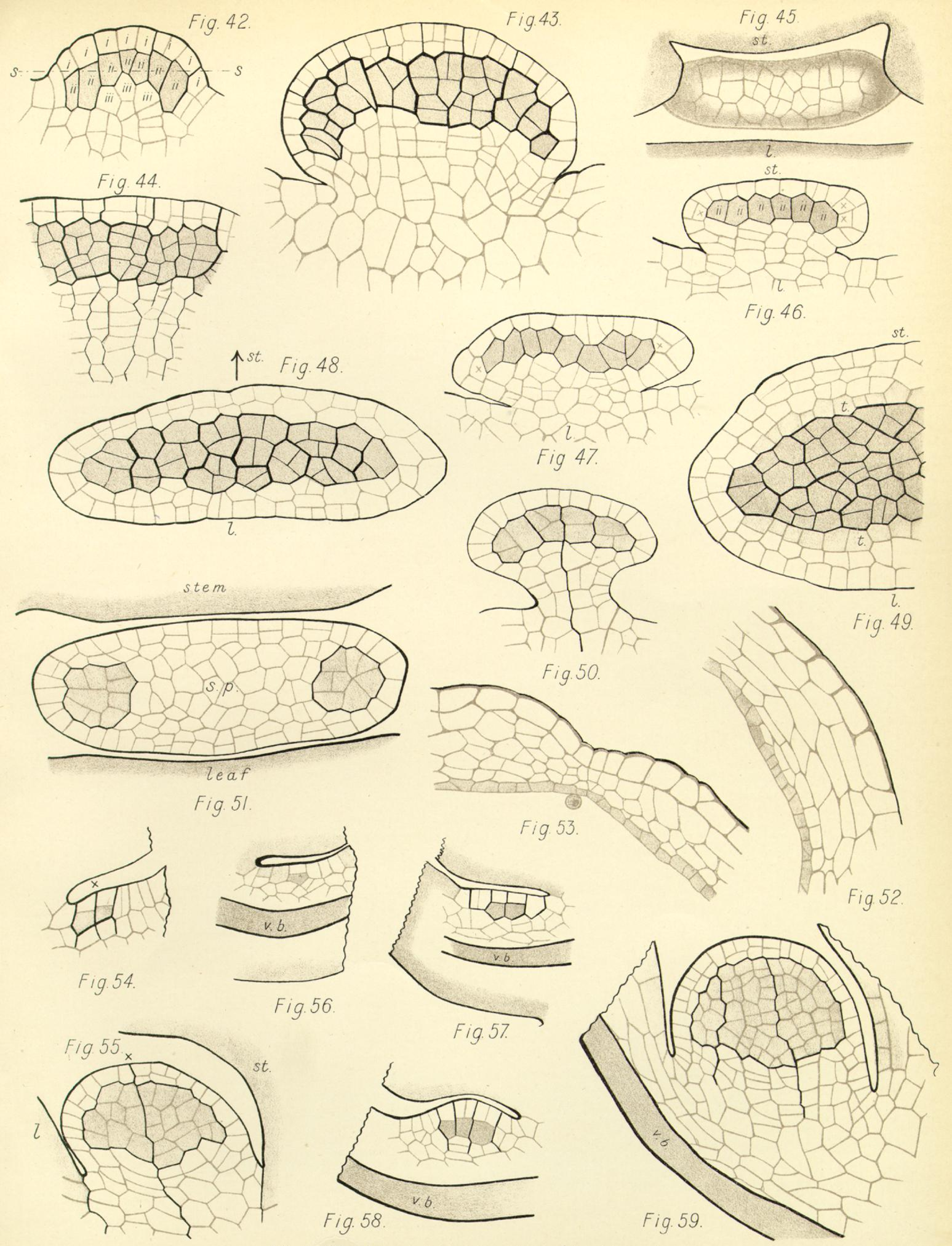
Fig. 37. Ditto, a more advanced stage; showing very regular segmentation. (× 300.)

Fig. 38. Ditto, showing a less regular type of segmentation. (× 300.)

Fig. 39. Ditto; still less regular. (× 300.)

Fig. 40. Ditto, older; the tapetum (*t.*) not yet complete. (× 150.)

Fig. 41. Ditto, older; showing the spore-mother-cells separated from one another, but not yet divided into tetrads. (× 150.)



FIGS 42–49. LYCOPODIUM SELAGO. L.
FIG. 50. L. PHLEGMARIA L. FIG. 51. L. CARINATUM DESV.
FIGS 52–53. L. DICHOTOMUM JACQ. FIGS 54–55. L. INUNDATUM L.
FIGS 56–59. L. CLAVATUM L.

PLATE 45.

Fig. 42. Tangential section of a young sporangium of *L. Selago*; the cells numbered i., ii., iii., correspond to those similarly numbered in fig. 36 (× 300.)

Fig. 43. Ditto, older. (× 300.)

Fig. 44. A small part of a similar section from a rather older sporangium. (× 300.)

Fig. 45. Young sporangium, seen in superficial view. (× 300.) *st.* = stem; *l.* = sporophyll.

Fig. 46. A sporangium of almost the same age seen in transverse section; compare the line in fig. 42; the archesporial cells are shaded in both figures, and numbered (ii.). (× 300.)

Fig. 47. Ditto. (× 300.)

Fig. 48. Ditto, older, before the tapetum is defined. (× 300.)

Fig. 49. Ditto; half of an older sporangium in which the formation of the tapetum (*t.*) is almost complete. (× 300.)

Lycopodium Phlegmaria, L.

Fig. 50. Tangential section of a young sporangium, showing the archesporium, referable to not more than four, and possibly to two cells. (× 300.)

Lycopodium carinatum, DESV.

Fig. 51. Transverse section of a sporangium, so as to traverse the sub-archesporial pad (*s.p.*); the two ends of the curved mass of sporogenous tissue are cut through, and are shaded; this is intended for comparison with a transverse section of the "fertile frond" of *Ophioglossum*. (× 300.)

Lycopodium dichotomum, JACQ.

Fig. 52. Part of the wall of sporangium in section; the tapetum is shaded. (× 150.)

Fig. 53. The same, showing the point of dehiscence. (× 150.)

Lycopodium inundatum, L.

Fig. 54. Radial section of a young sporangium, showing periclinal division in two distinct cells; two archesporial cells are shaded. (× 300.)

Fig. 55. A similar section of an older sporangium. (× 300.)

Lycopodium clavatum, L.

Fig. 56. Radial section through a very young sporangium, showing the first periclinal division. (× 300.)

Fig. 57. Ditto, showing periclinal divisions in two distinct cells. (× 300.)

Fig. 58. Ditto, older, showing result of periclinal division in three cells; the archesporium thus defined is shaded. (× 300.)

Fig. 59. Older sporangium, in radial section, with large sporogenous tissue, so grouped as to be still referable to three original cells; compare fig. 58. (× 300.)

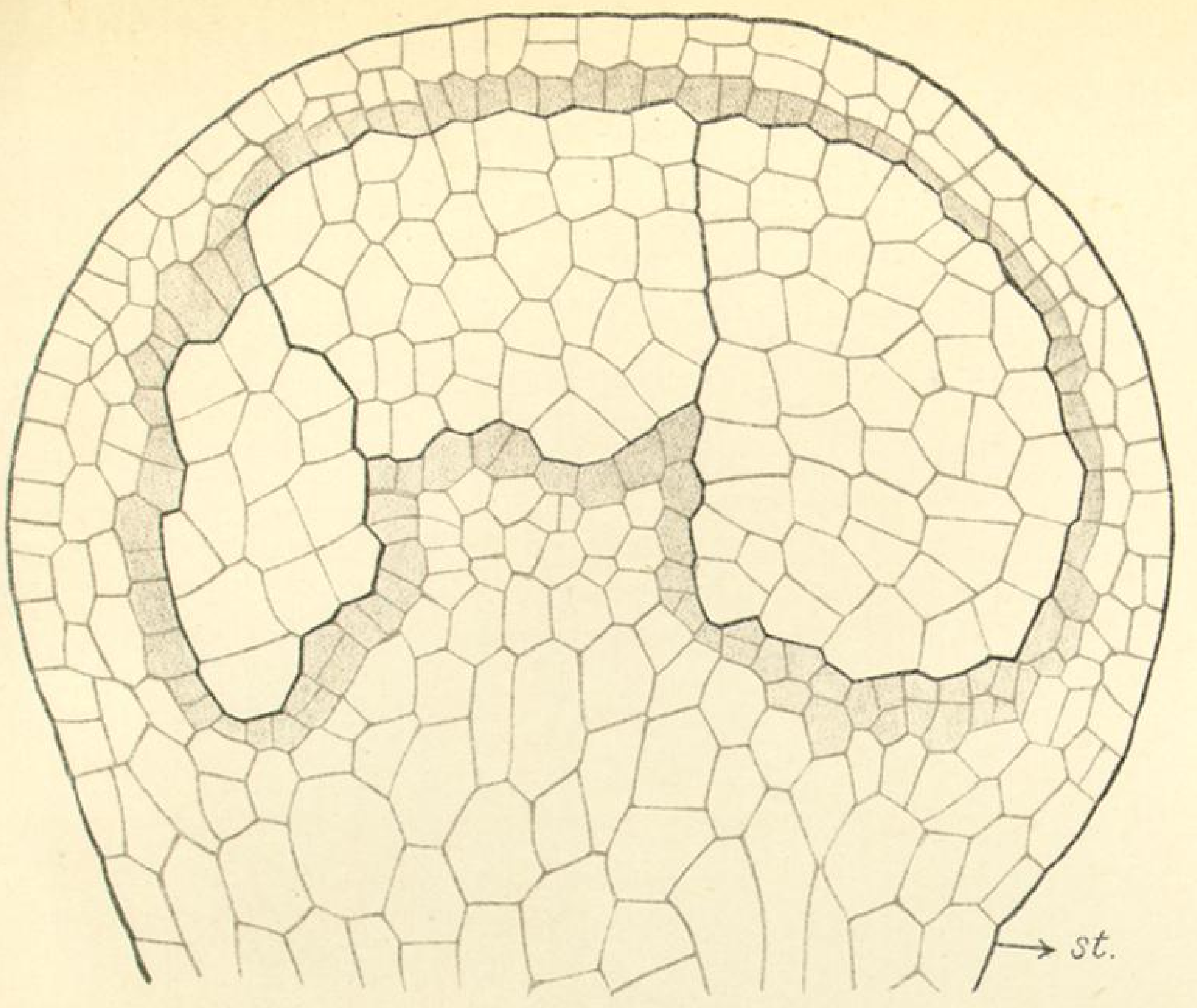


Fig. 60.

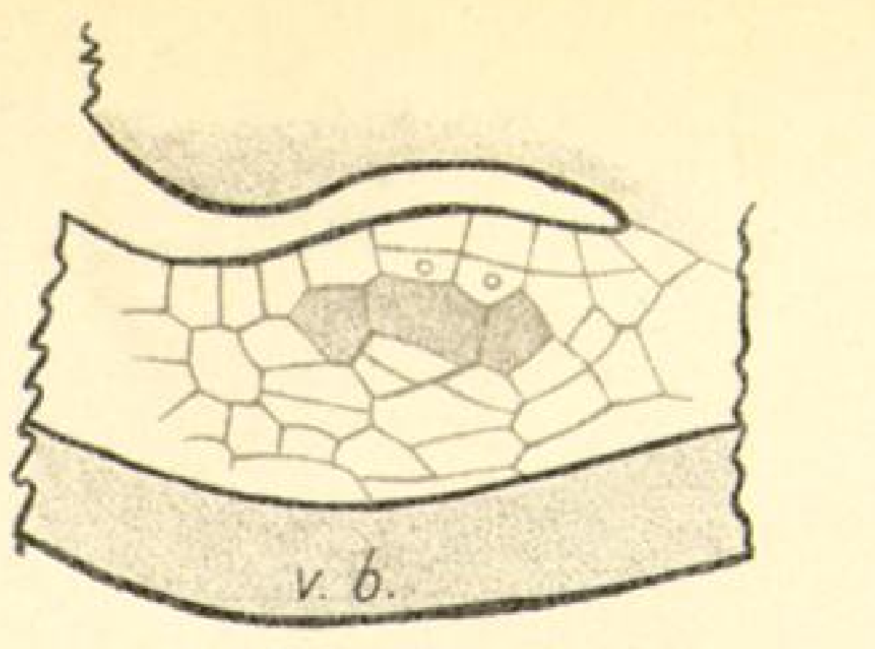
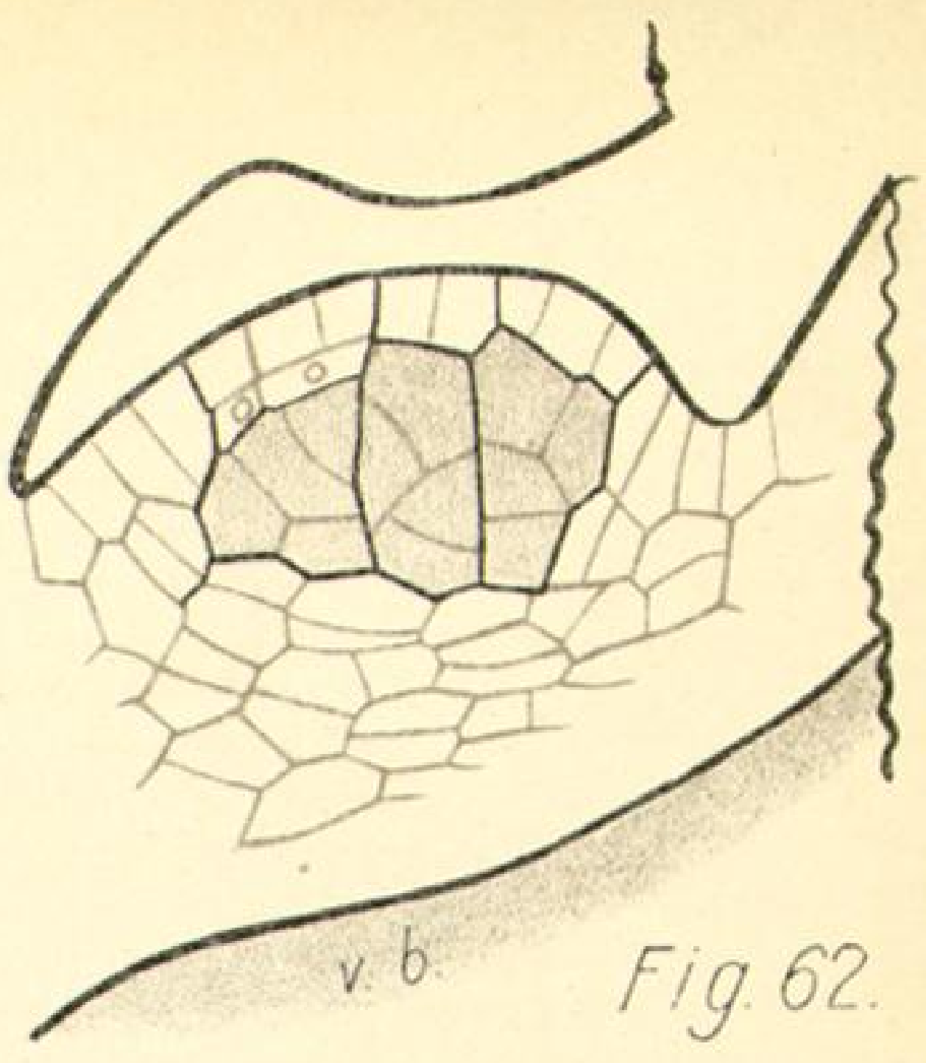


Fig. 61.



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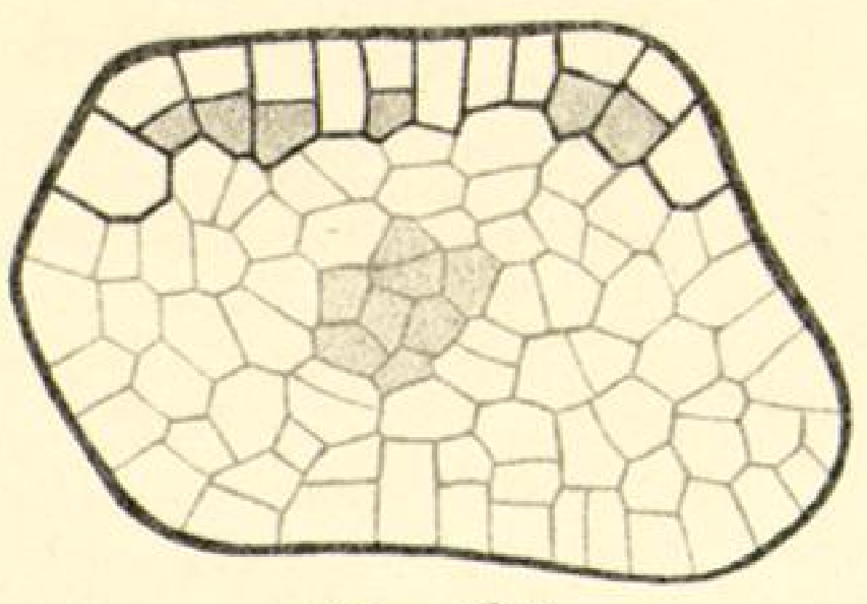

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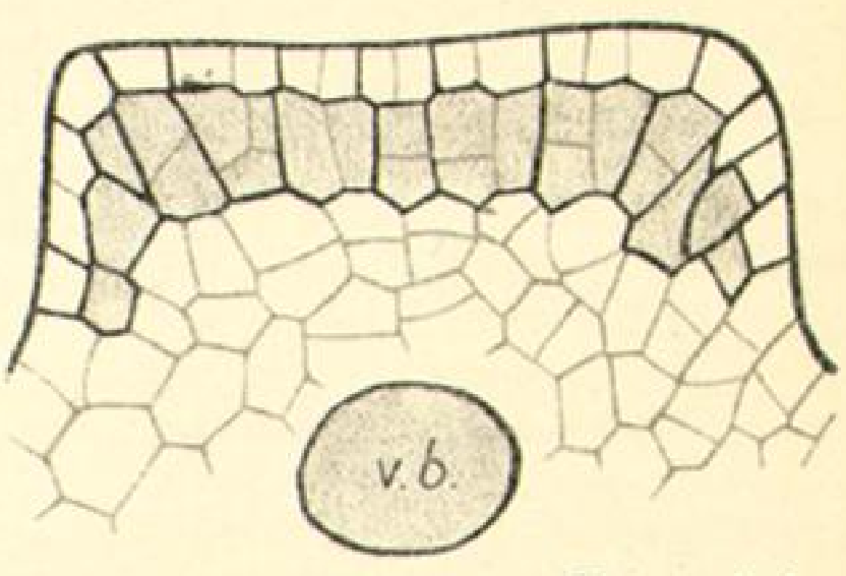
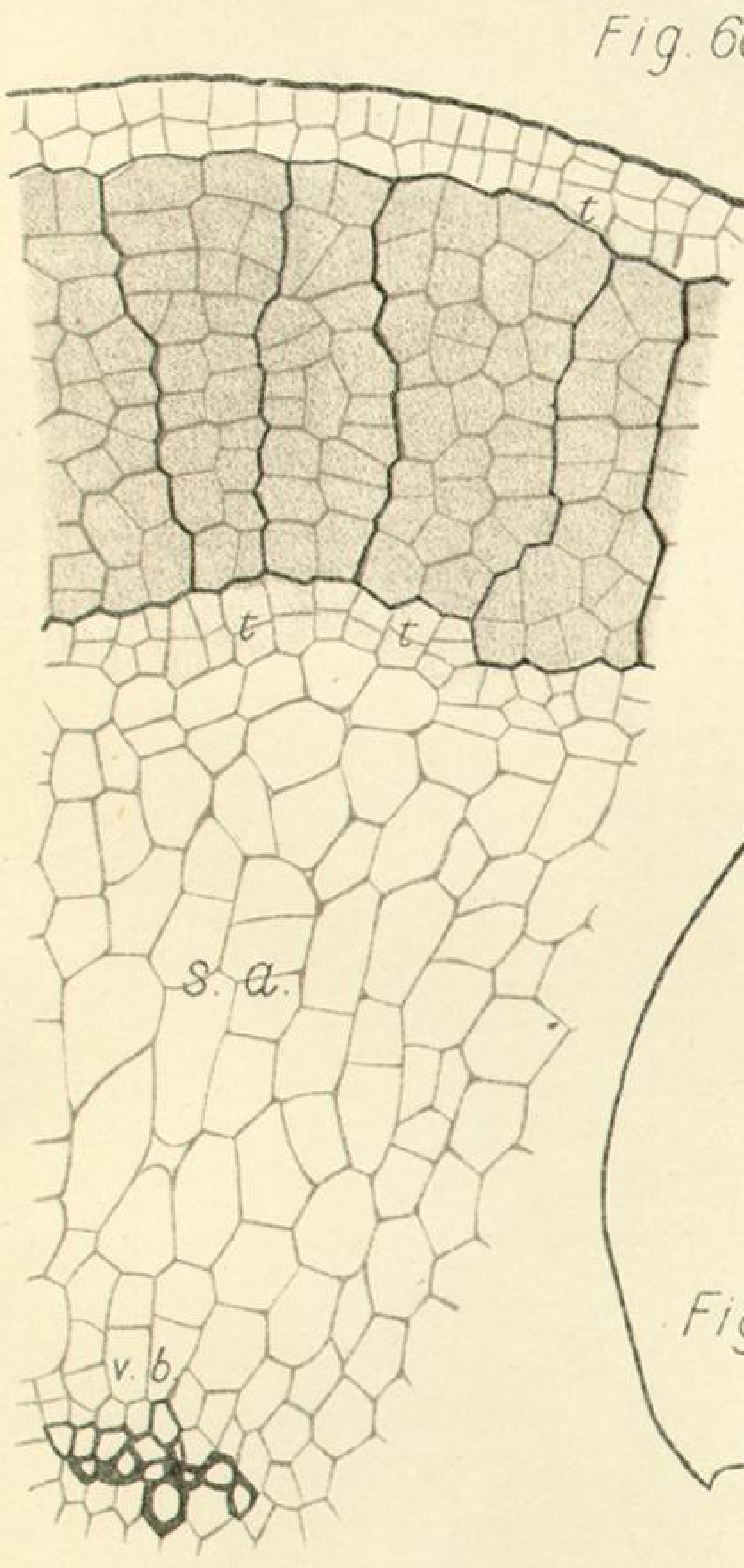


Fig. 64.



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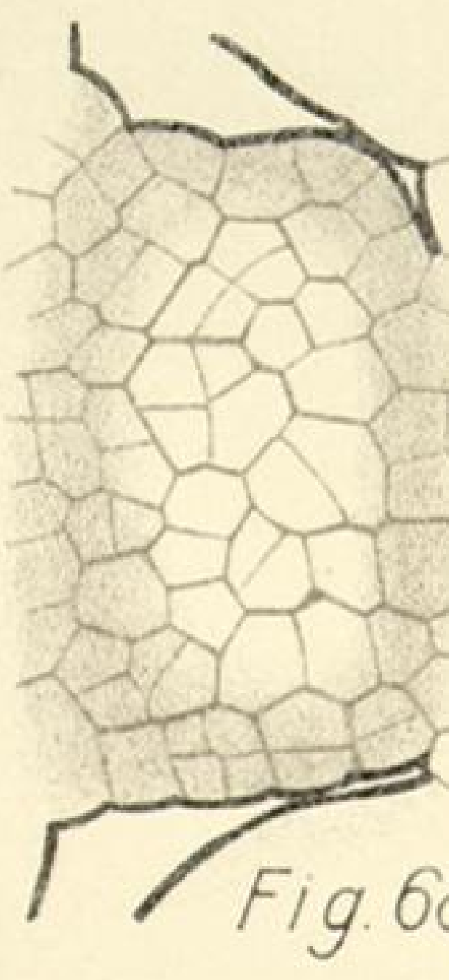

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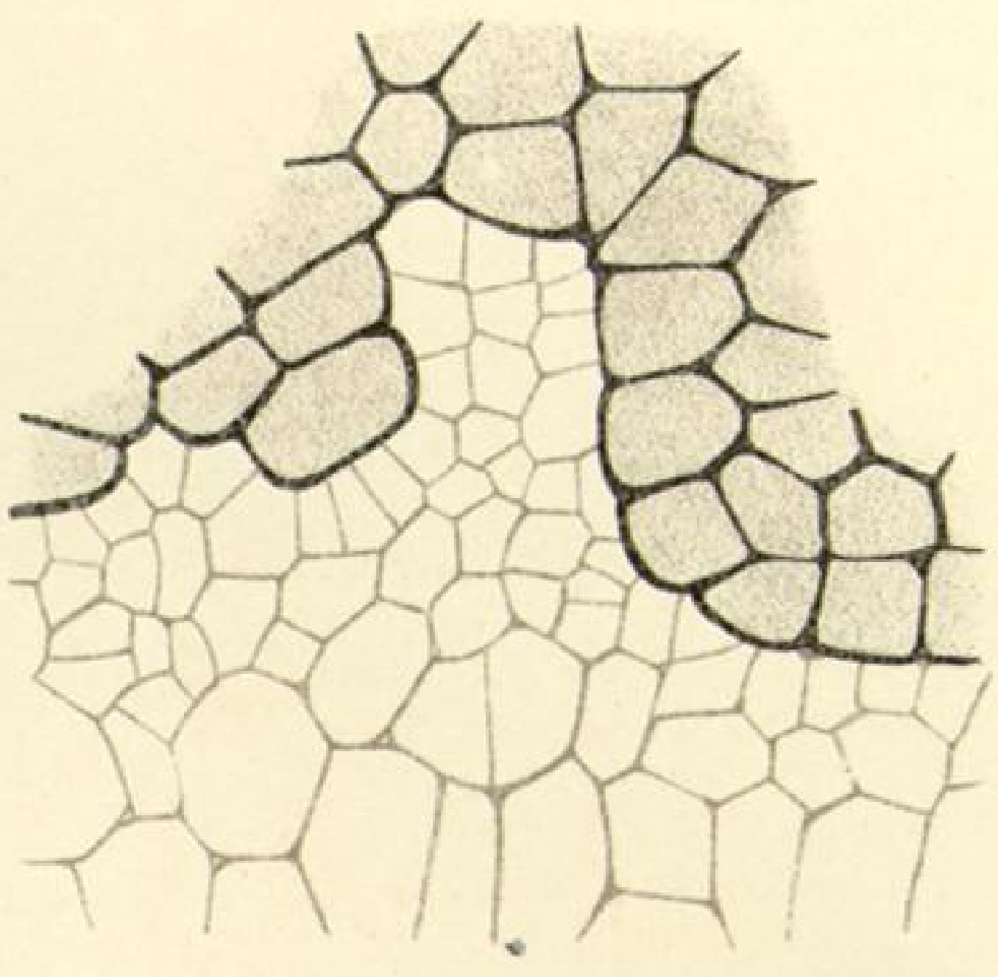

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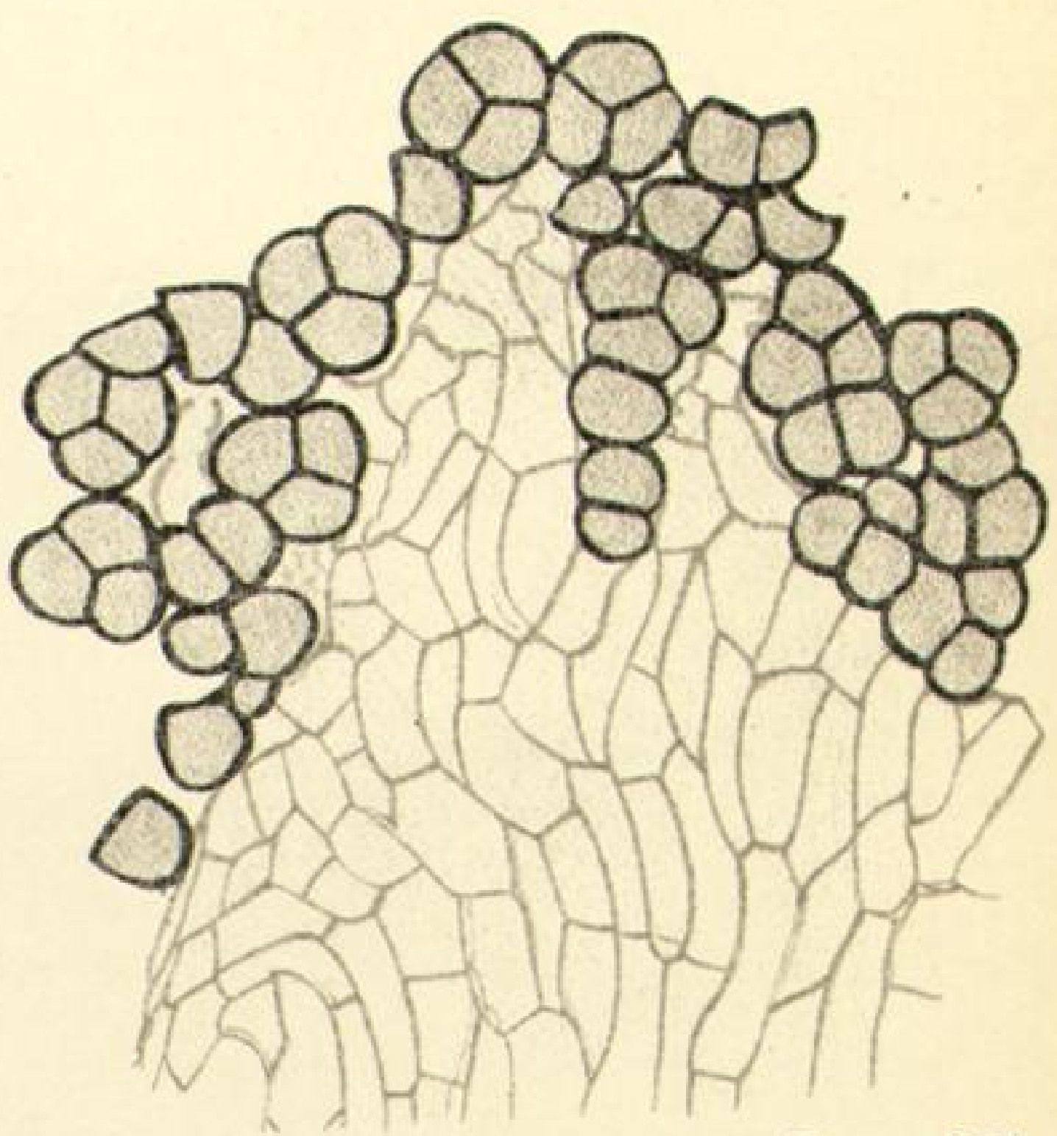

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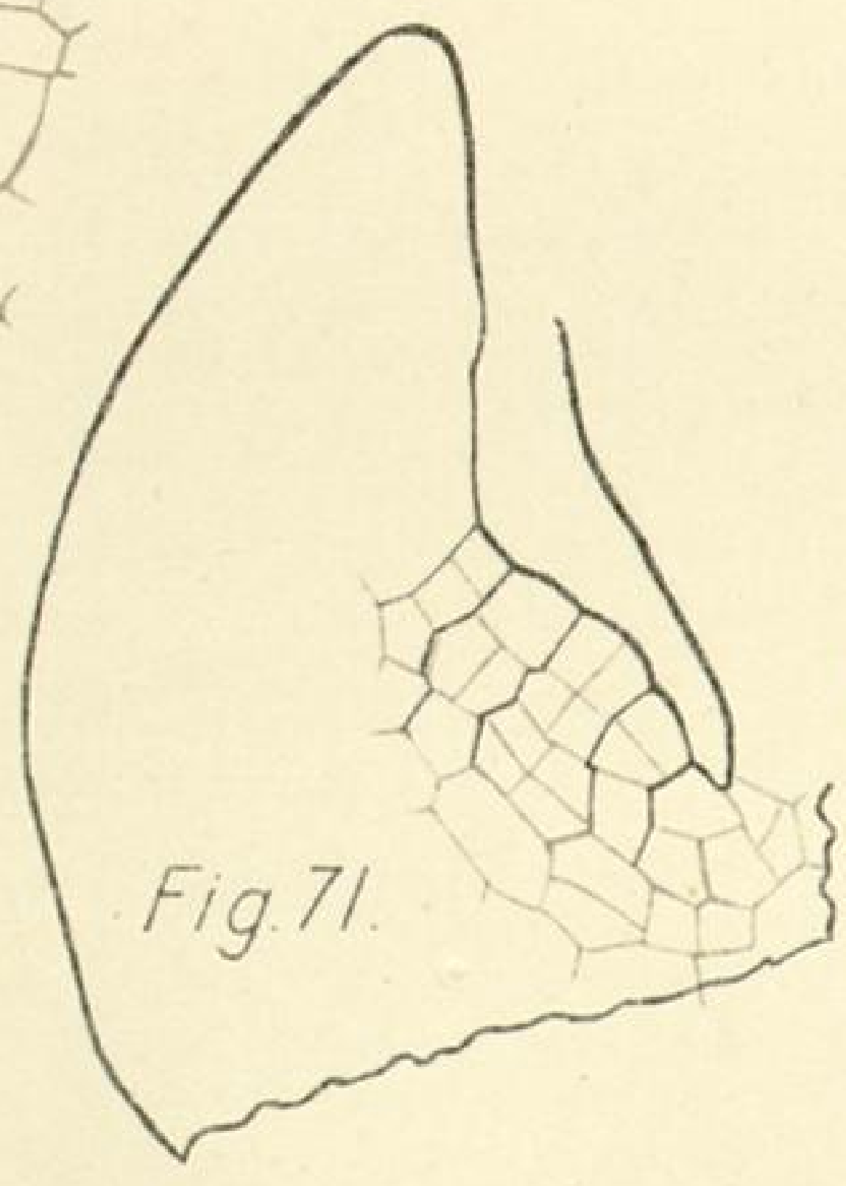

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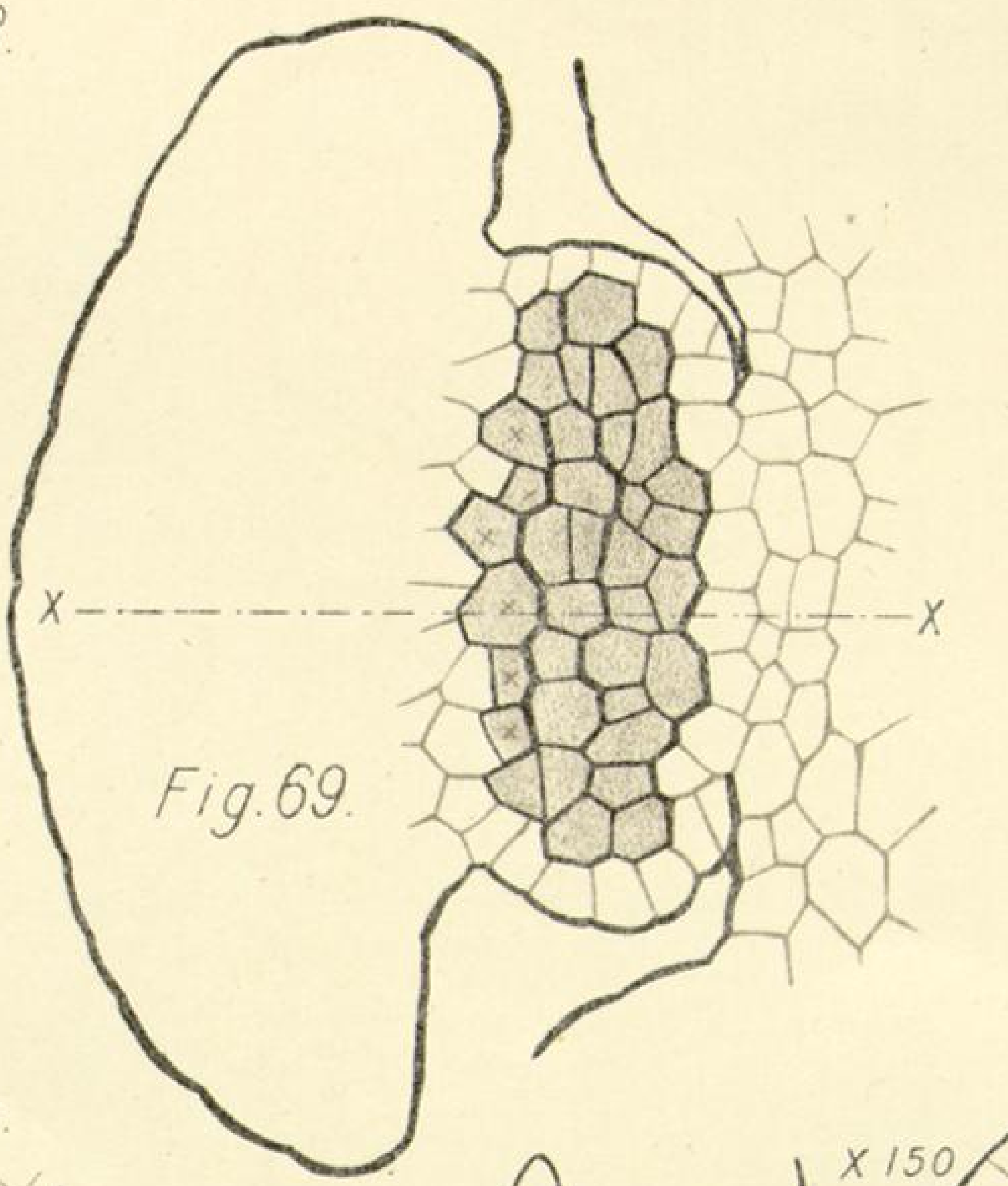


Fig. 69.

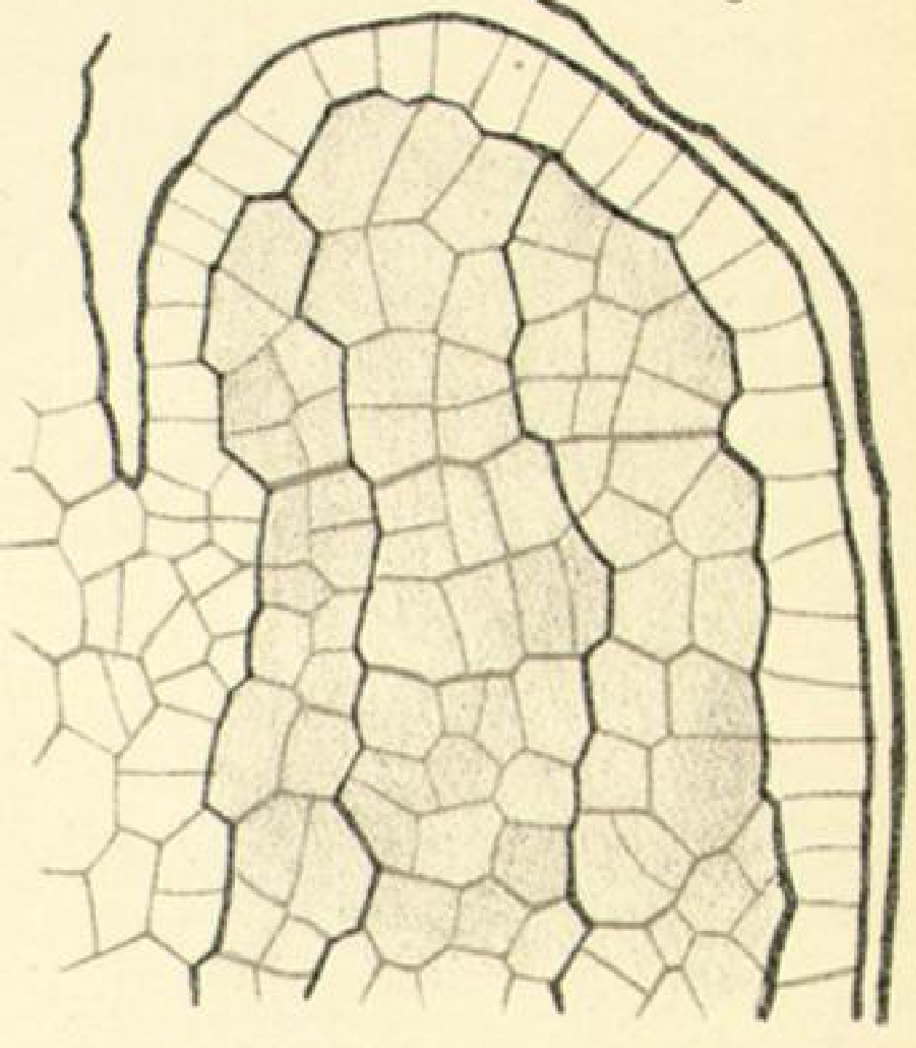


Fig. 70.

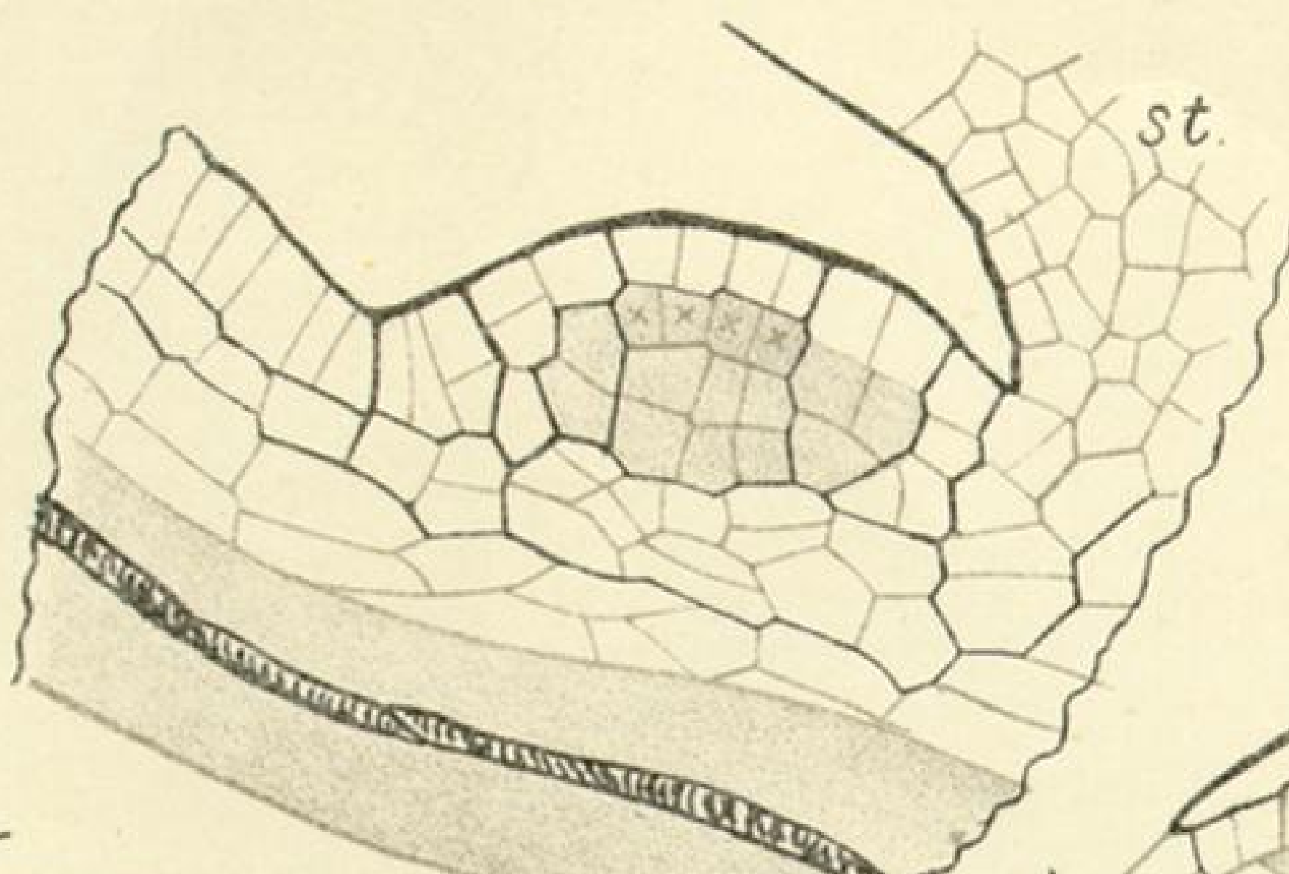
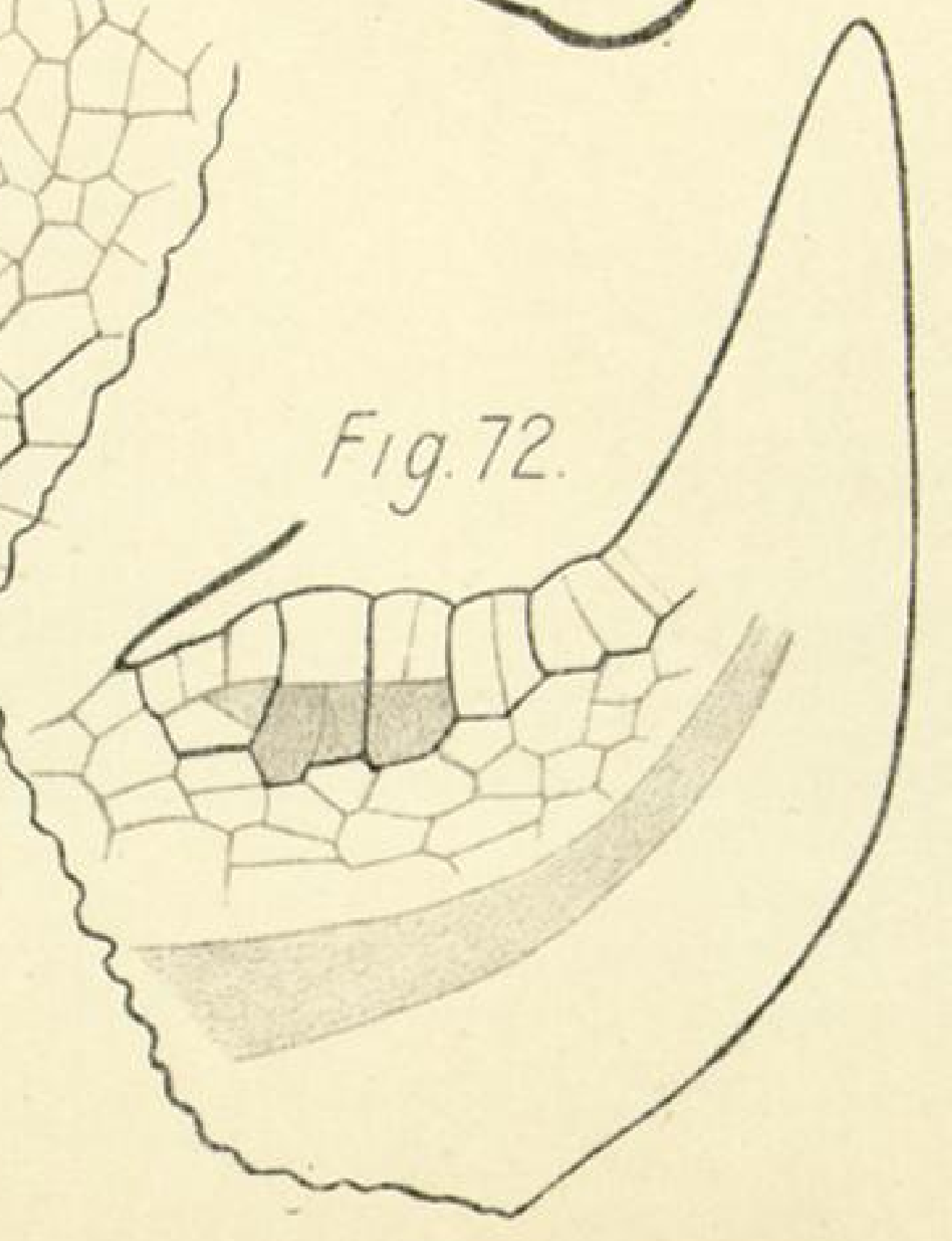


Fig. 74.



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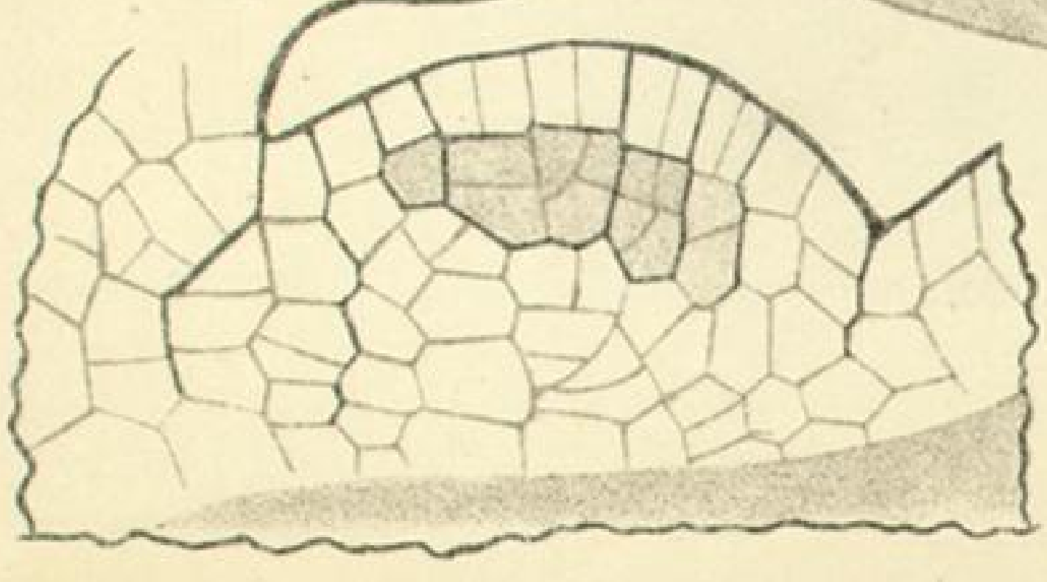


Fig. 73.

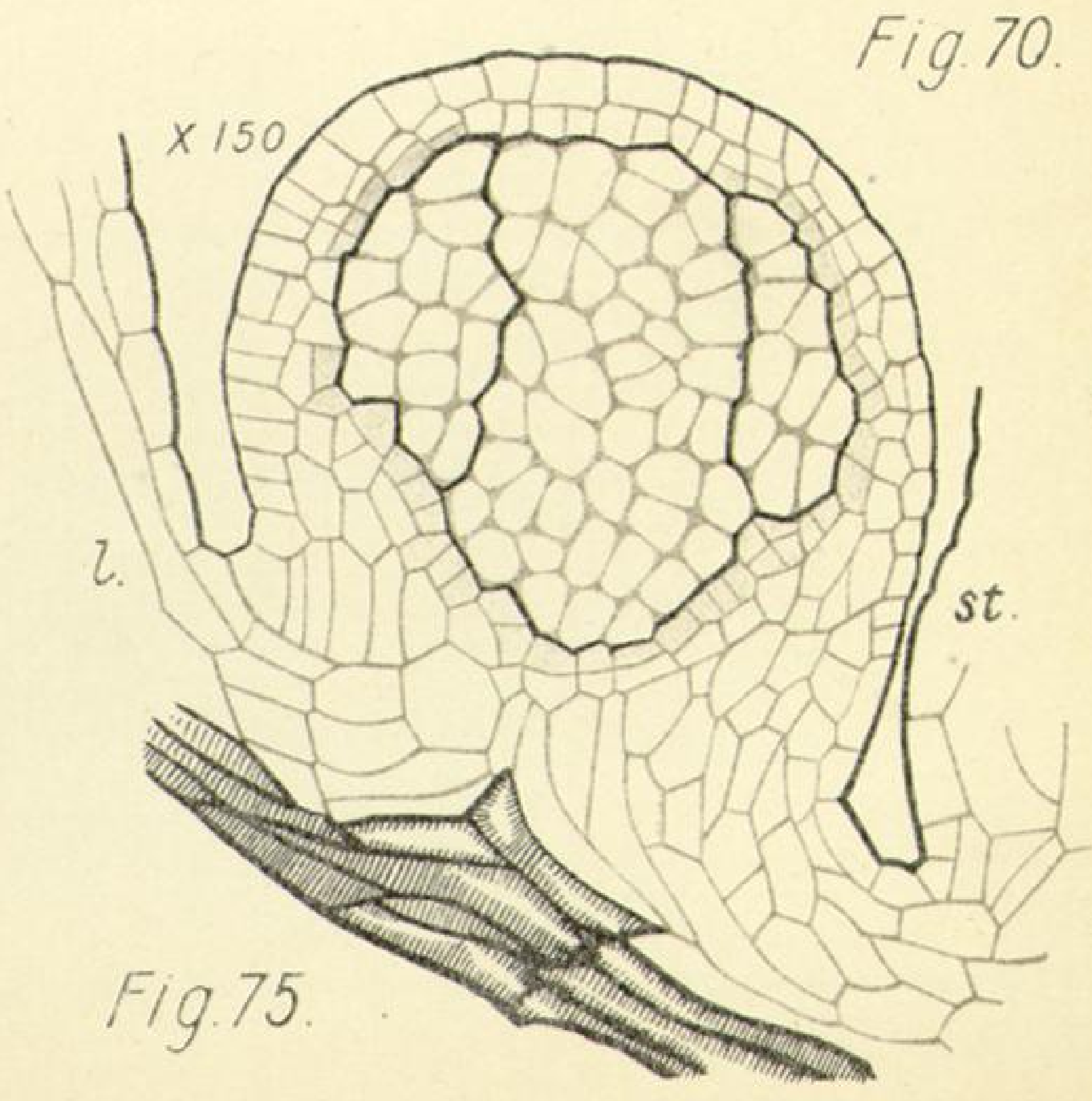


Fig. 75.

Figs 60–70 LYCOPODIUM CLAVATUM. L.
Figs 71–75 „ ALPINUM. L.

PLATE 46.

Fig. 60. Radial section of an older sporangium; *st.* = the adaxial side: the sporogenous tissue not shaded, it is still referable to the three parent cells, the lower limit of the groups being here unusually irregular. The tapetum is shaded. (× 300).

Fig. 61. Radial section of a sporangium, which shows early periclinal divisions of the superficial cells; the fate of the inner cells (*o*, *o*) is uncertain; *v.b.* = vascular bundle. (× 300.)

Fig. 62. Ditto. (× 300.)

Fig. 63. Tangential section of a sporophyll bearing a sporangium of age corresponding to that in fig. 56; the periclinal walls have not yet appeared in all the parent cells of the sporangium. (× 300.)

Fig. 64. A similar section of an older sporangium; in both of these the archesporium is shaded. (× 300.)

Fig. 65. Part of a tangential section of an older sporangium; *t.* = tapetum; *v.b.* = vascular bundle; *s.a.* = sub-archesporial pad; sporogenous tissue is deeply shaded. (× 300.)

Fig. 66. Small part of the sub-archesporial tissue, showing a process rising upwards into the mass of spore-mother-cells. (× 300.)

Fig. 67. A similar part from an almost mature sporangium; the irregular upward processes are now partly disorganized. (× 150.)

Fig. 68. View of the superficial cell-net of a sporangium, as seen from above. (× 300.)

Fig. 69. Transverse section of such a sporangium traversing the archesporium, which is shaded. (× 300.)

Fig. 70. Transverse section of an older sporangium; the three rows of parent cells of the sporogenous tissue may be still recognized. (× 300.)

Lycopodium alpinum, L.

Fig. 71. Radial section through a sporophyll and young sporangium. (× 300.)

Fig. 72. Ditto, the archesporium shaded. (× 300.)

Fig. 73. Ditto, rather older. (× 300.)

Fig. 74. Ditto, the cells marked (×) have apparently been derived by extra periclinal divisions from the superficial cells. (× 300.)

Fig. 75. Radial section of an older sporangium in which the spore-mother-cells are about to separate. The vascular bundle shows a slight extension upwards into the stalk of the sporangium. (× 150.)

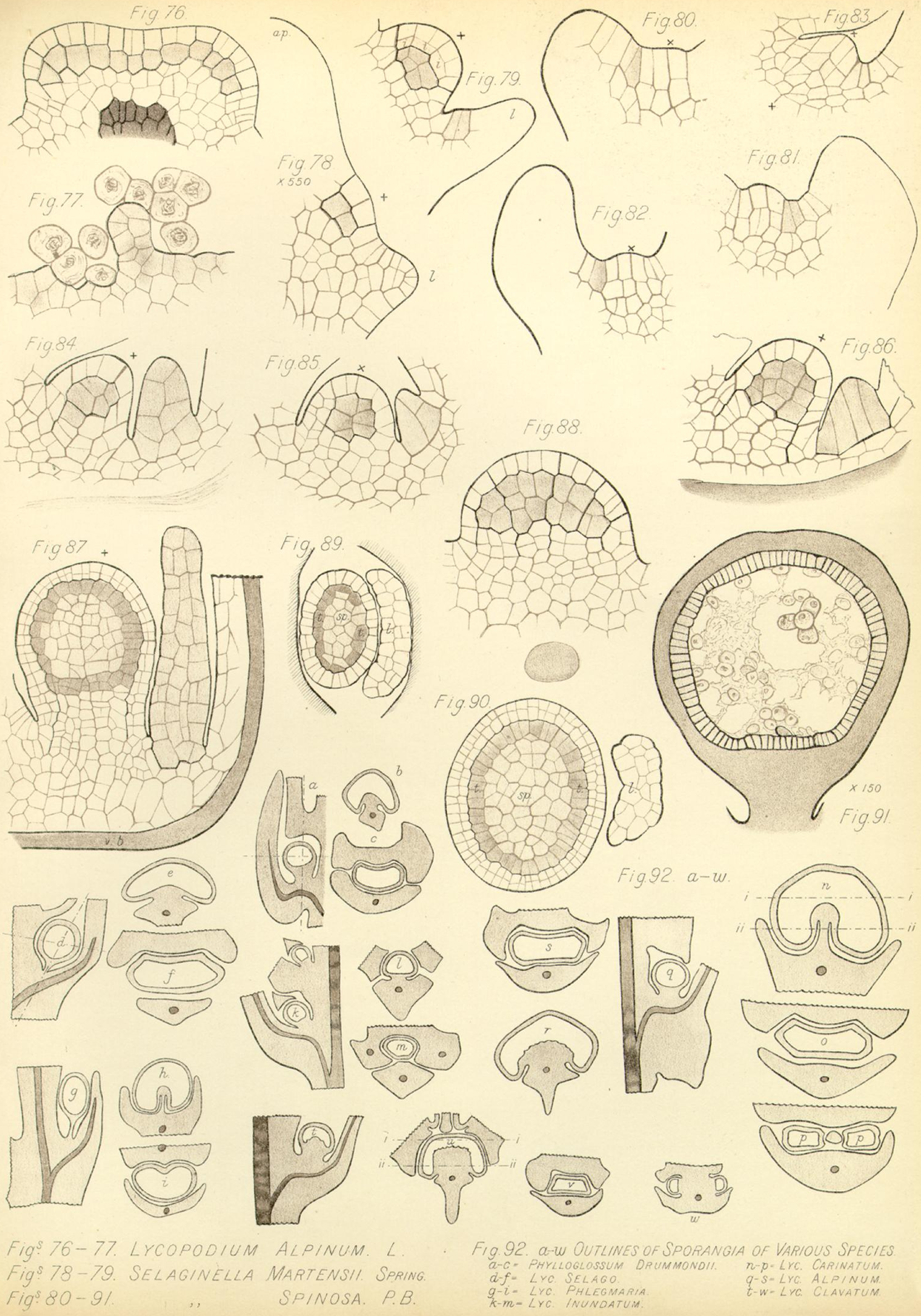


Fig. 76
Fig. 77
ap.
Fig. 78
x 550
l
Fig. 79
l
Fig. 80
Fig. 81
Fig. 82
Fig. 83
Fig. 84
Fig. 85
Fig. 86
Fig. 87
Fig. 88
Fig. 89
sp.
t
l
Fig. 90
sp
t
l
v.b
x 150
Fig. 91
Fig. 92. a–w.
a
b
c
d
e
f
g
h
i
k
l
m
n
o
p
q
r
s
t
u
v
w
Figs 76–77. Lycopodium alpinum. L.
Figs 78–79. Selaginella Martensii. Spring.
Figs 80–91. ,, spinosa. P.B.
Fig. 92. a-w Outlines of Sporangia of Various Species.
a-c = Phylloglossum Drummondii.
d-f = Lyc. Selago.
g-i = Lyc. Phlegmaria.
k-m = Lyc. Inundatum.
n-p = Lyc. Carinatum.
q-s = Lyc. Alpinum.
t-w = Lyc. Clavatum.

PLATE 47.

Fig. 76. Tangential section through a young sporangium, showing an archesporium consisting of twelve cells, which are shaded. (× 300.)

Fig. 77. An upgrowth of the sub-archesporial tissue as a process, which projects between the sporogenous cells. (× 300.)

Selaginella Martensii, Spring.

Fig. 78. Radial section, including apex (*ap.*), and traversing a young sporophyll (*l*) and sporangium (*x*). (× 550.)

Fig. 79. Ditto, rather older. (× 550.)

Selaginella spinosa, P.B.

Fig. 80. Radial section through a very young sporangium. (× 550.)

Fig. 81. Ditto. (× 550.)

Fig. 82. Ditto. (× 550.)

Fig. 83. Ditto. (× 550.)

Figs. 84–86. Ditto, older. (× 550.)

Fig. 87. Ditto, a good deal older, showing all the essential parts of the sporangium together with ligule, and part of sporophyll. (× 300.)

Fig. 88. Tangential section of a sporangium of about the same age as figs. 84–86: the archesporium is referable apparently to four parent cells. (× 550.)

Figs. 89–90. Transverse sections of sporangia of two different ages. *l.* = ligule, *t.* = tapetum, *sp.* = sporogenous tissue. (× 300.)

Fig. 91. Radial section of a megasporangium showing the single tetrad still very small, and the rest of the potential sporogenous cells arrested. (× 150.)

Fig. 92. *a–w*. Low-power drawings, showing outlines of the sporangia of various species, in radial, tangential, and transverse sections, together with parts of the sporophylls: *a, b, c, Phylloglossum Drummondii*; *d, e, f, L. Selago*; *g, h, i, L. phlegmaria*; *k, l, m, L. inundatum*; *n, o, p, L. carinatum*; *q, r, s, L. alpinum*; *t, u, v, w, L. clavatum*. (× 18.)

Fig. 93.

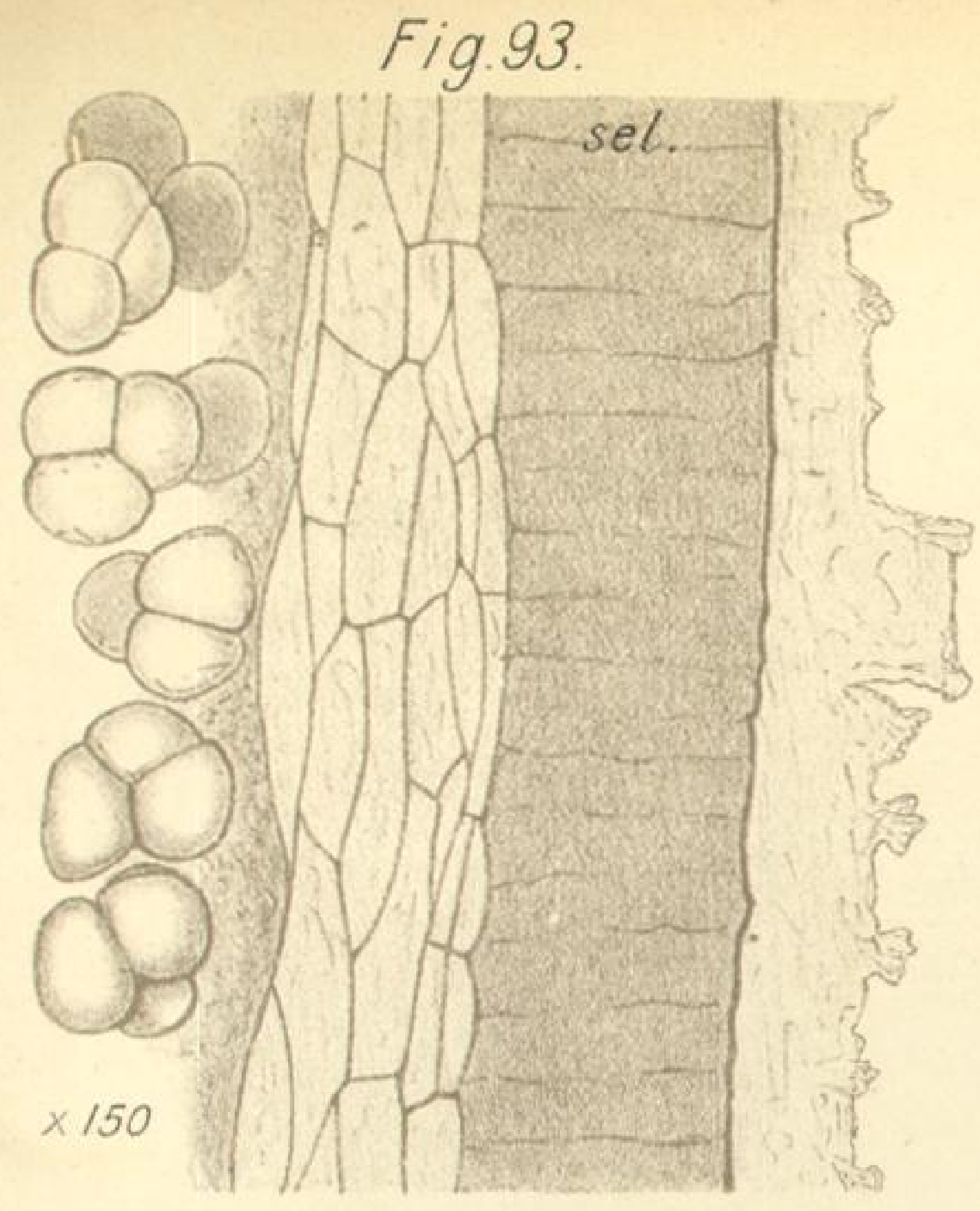


Fig. 94.

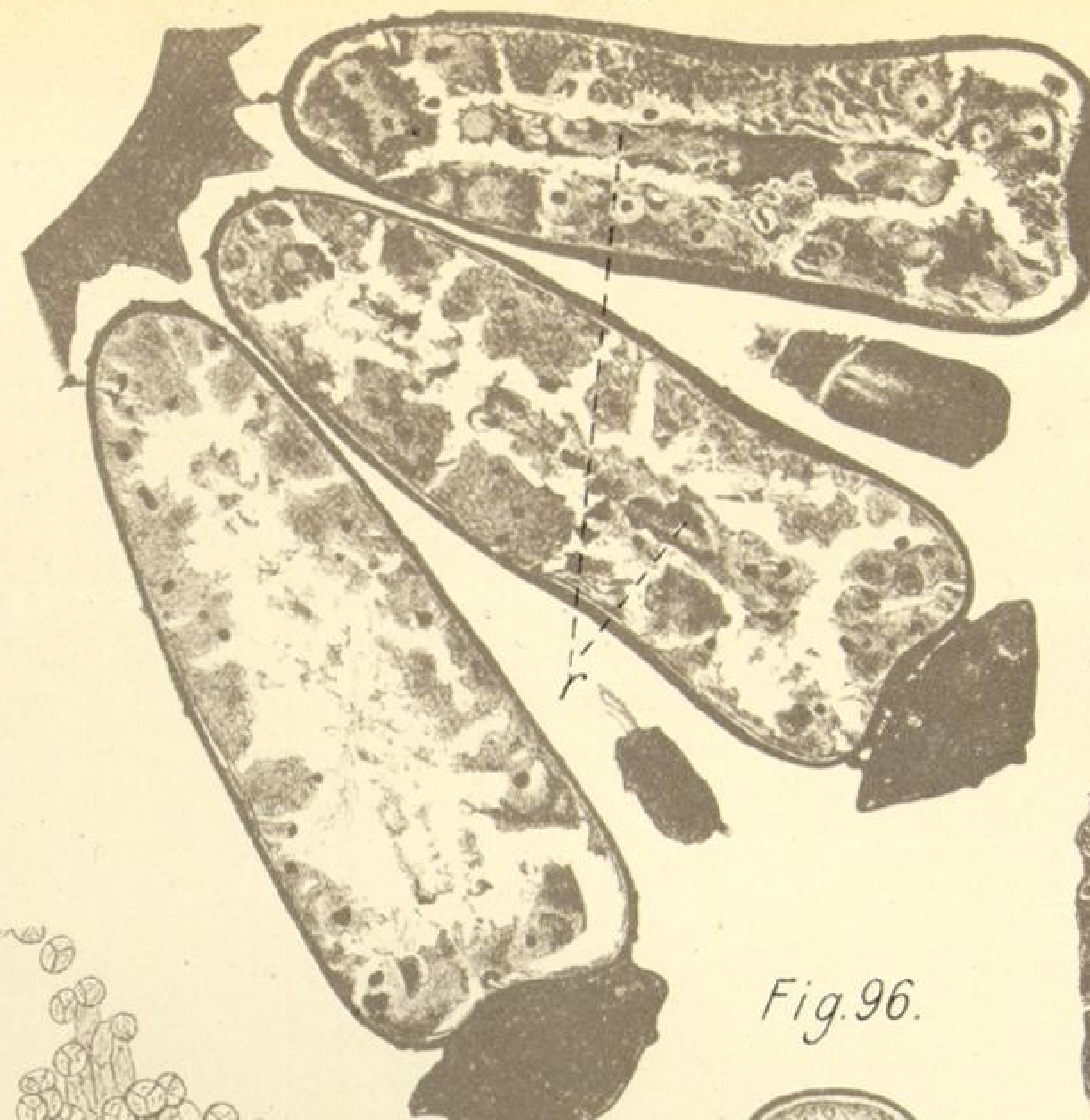


Fig. 95.

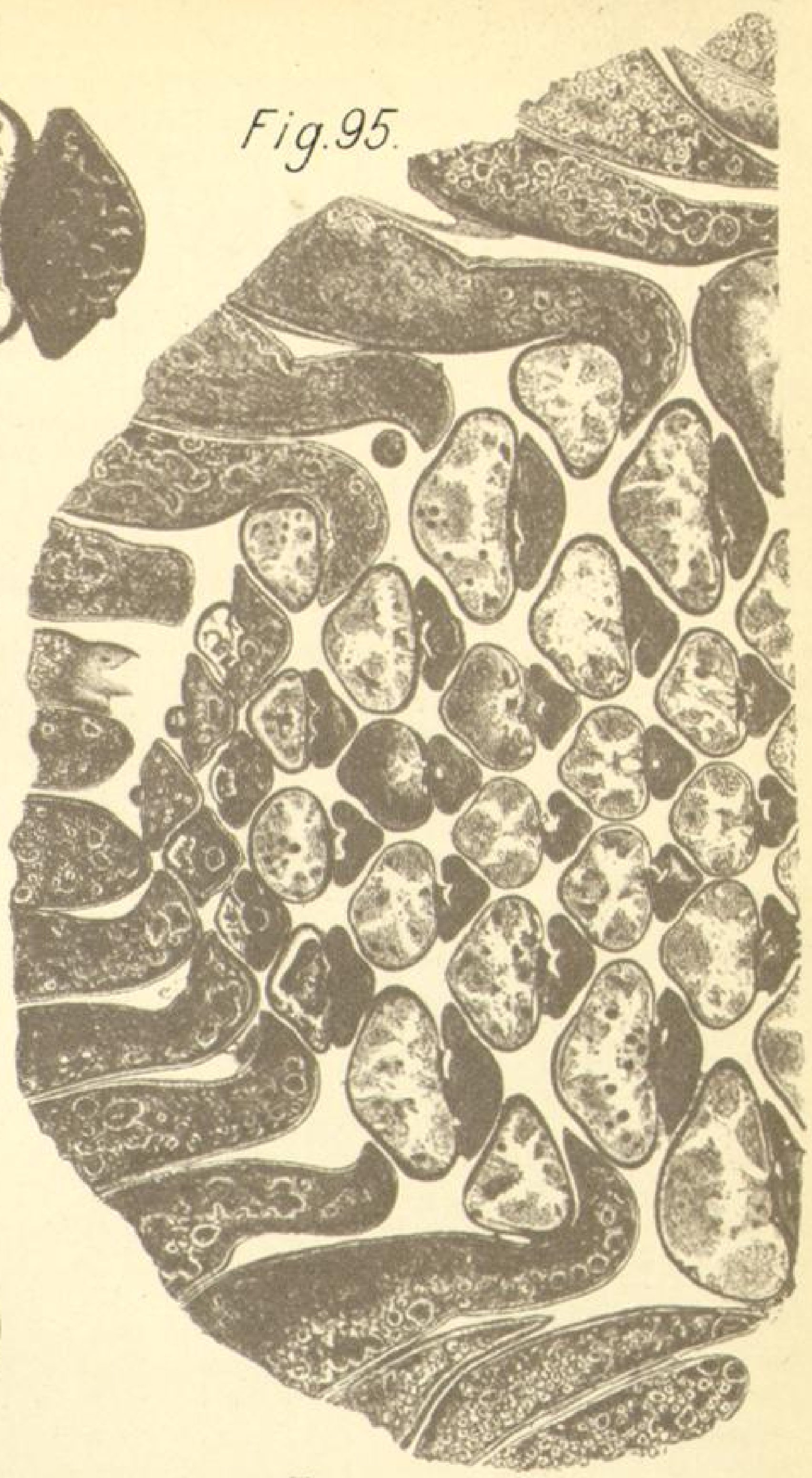


Fig. 97.

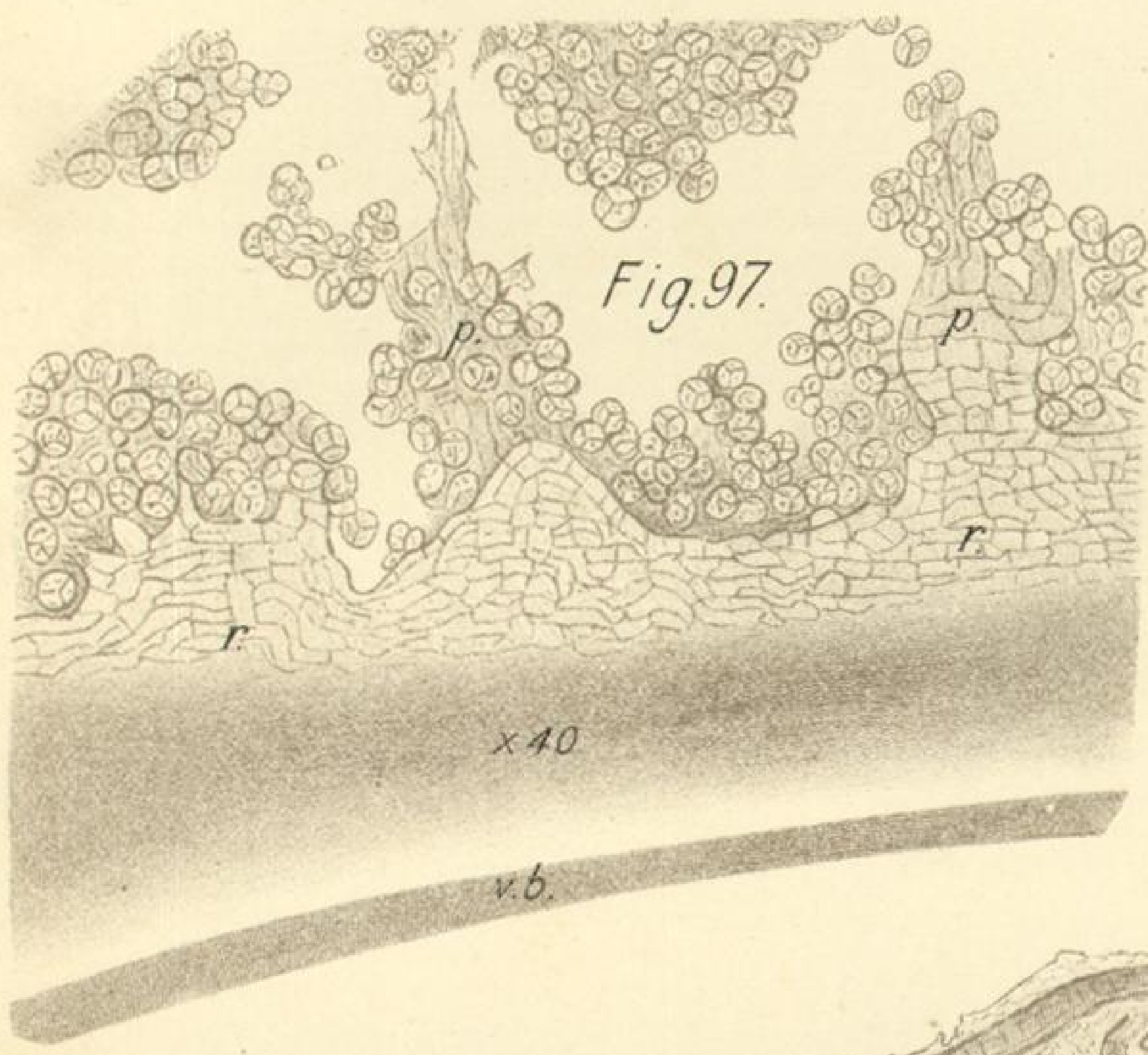


Fig. 96.

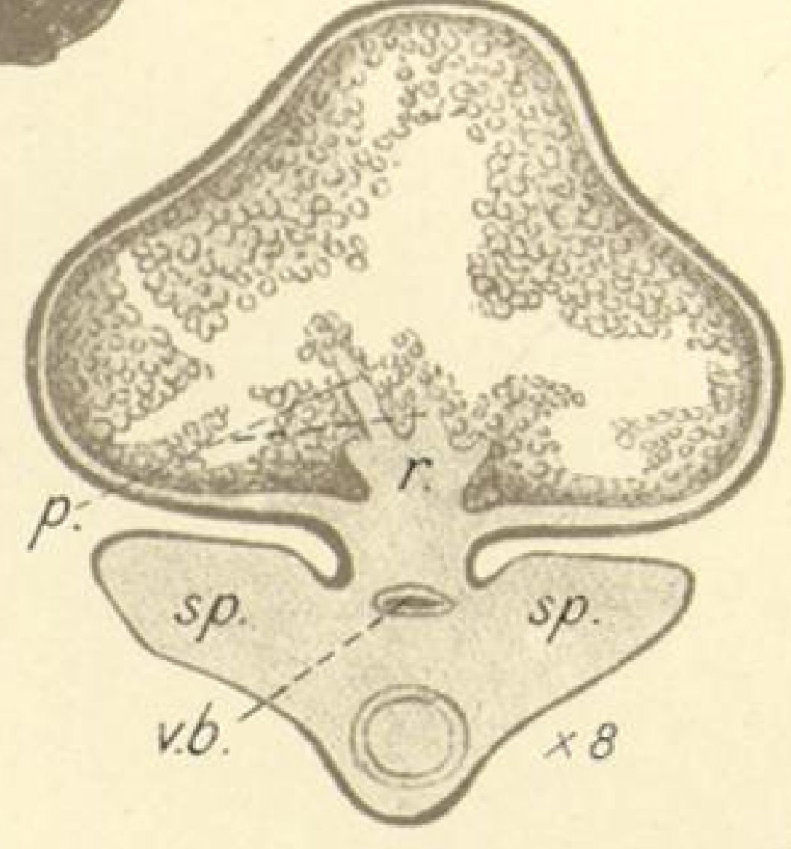


Fig. 100.

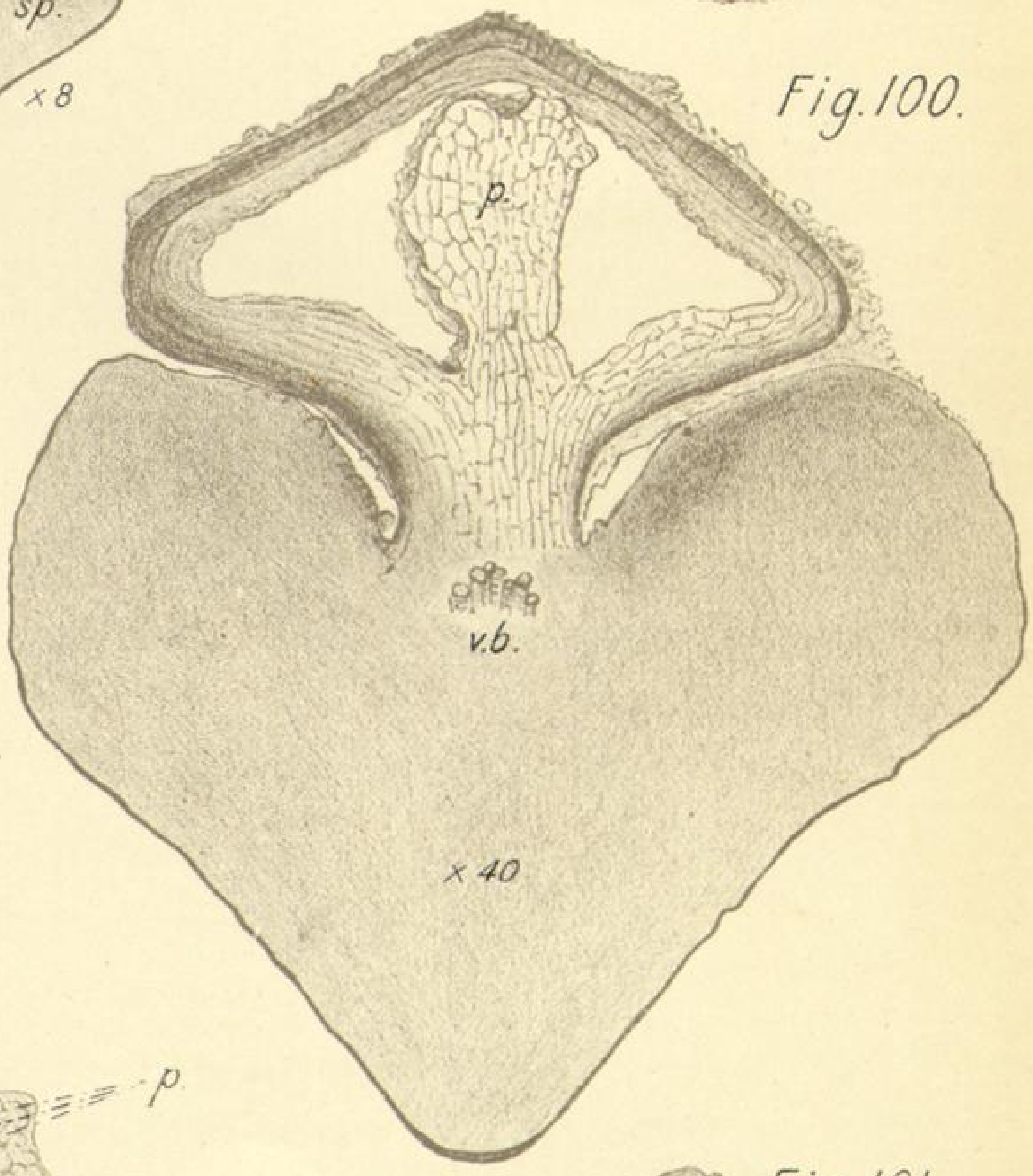


Fig. 99.

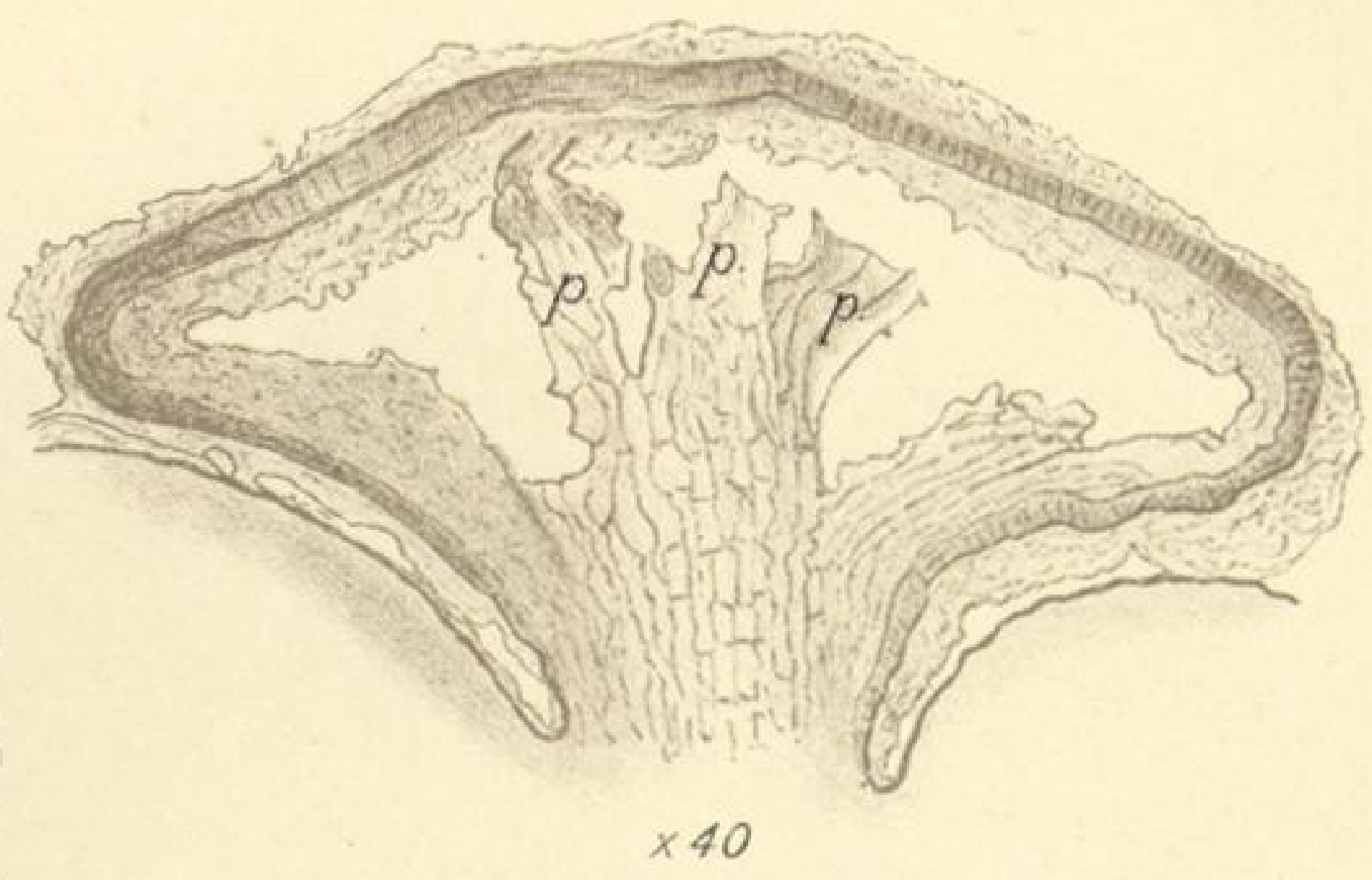


Fig. 98.

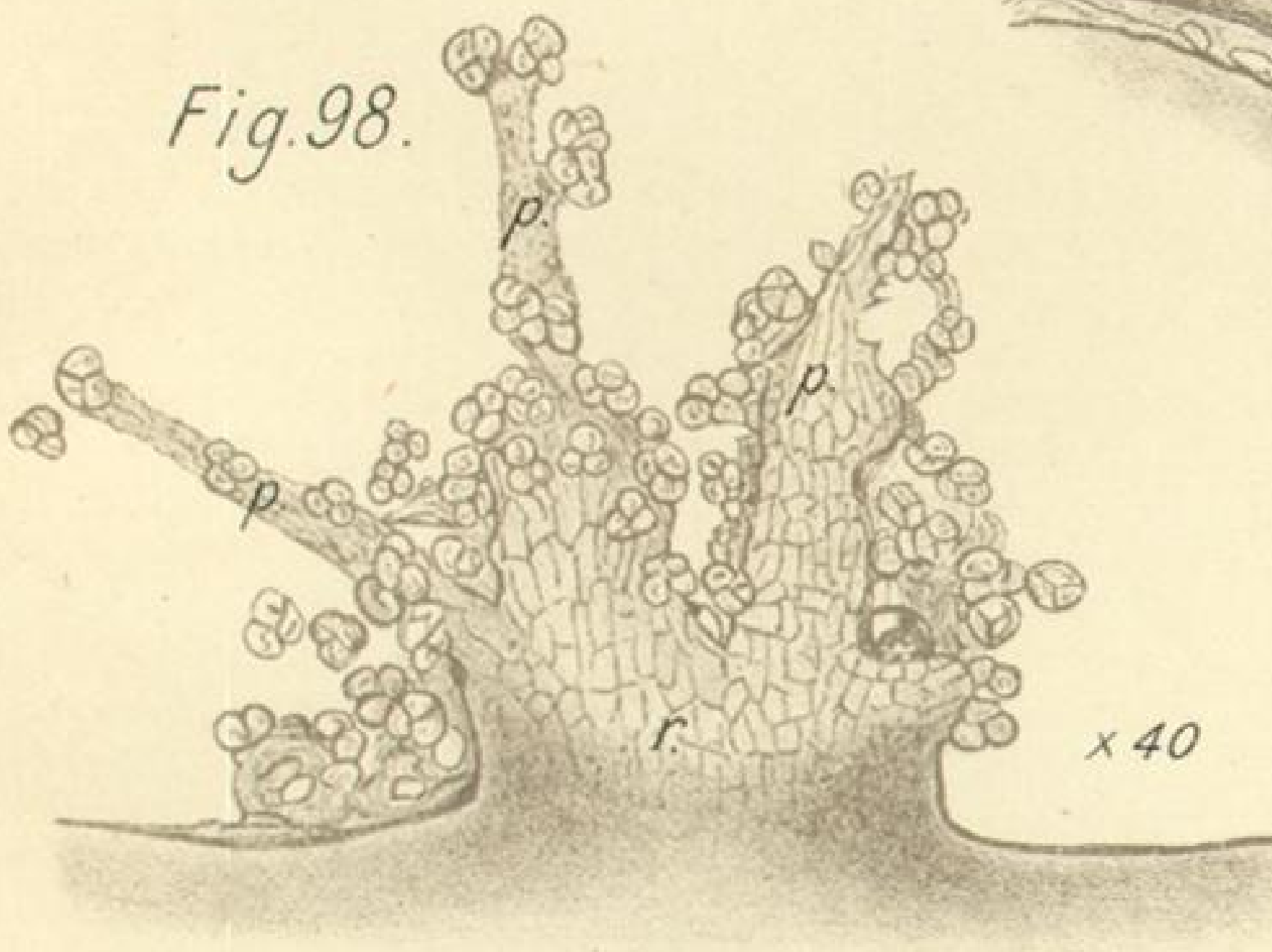


Fig. 103.

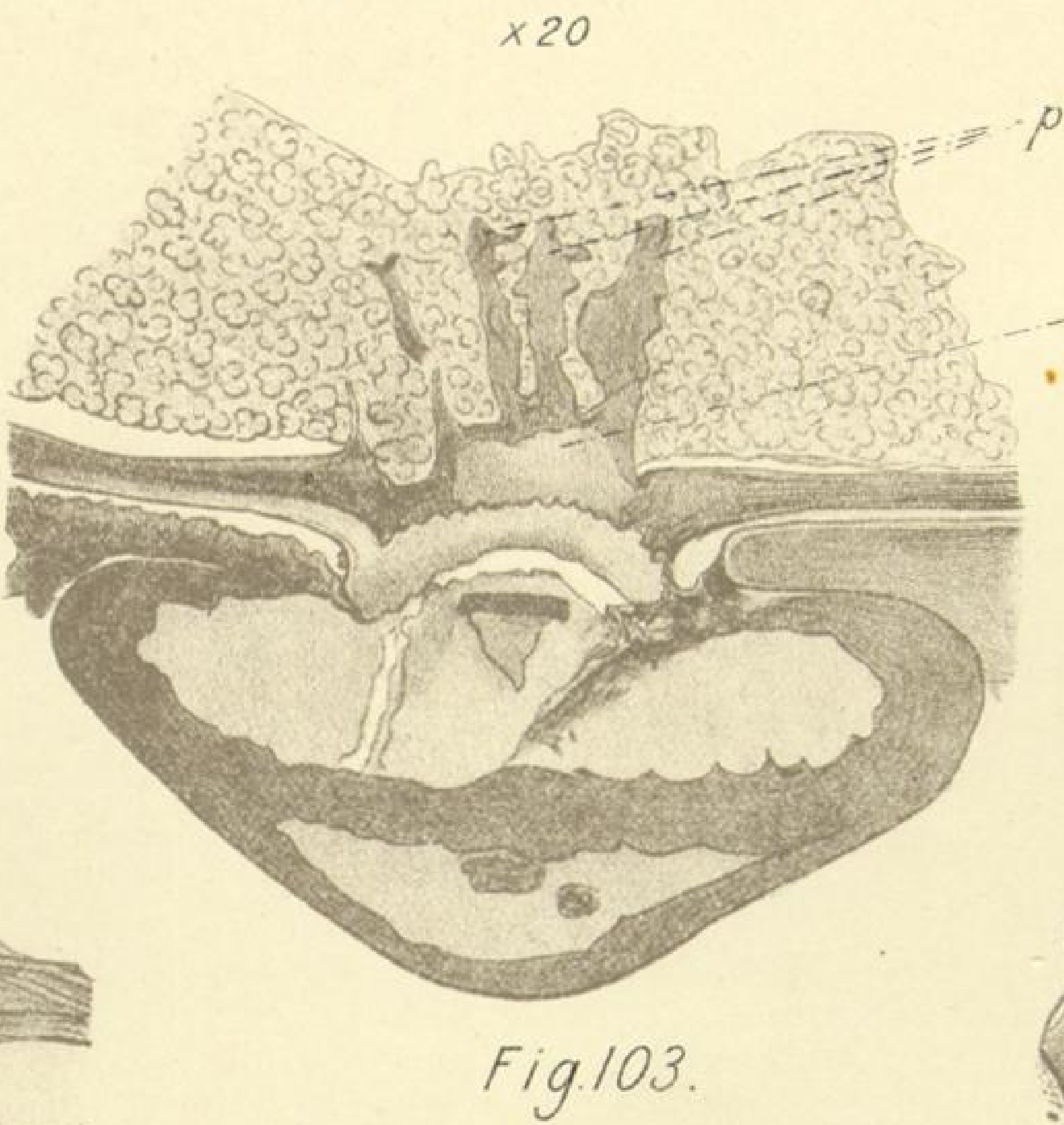


Fig. 101.

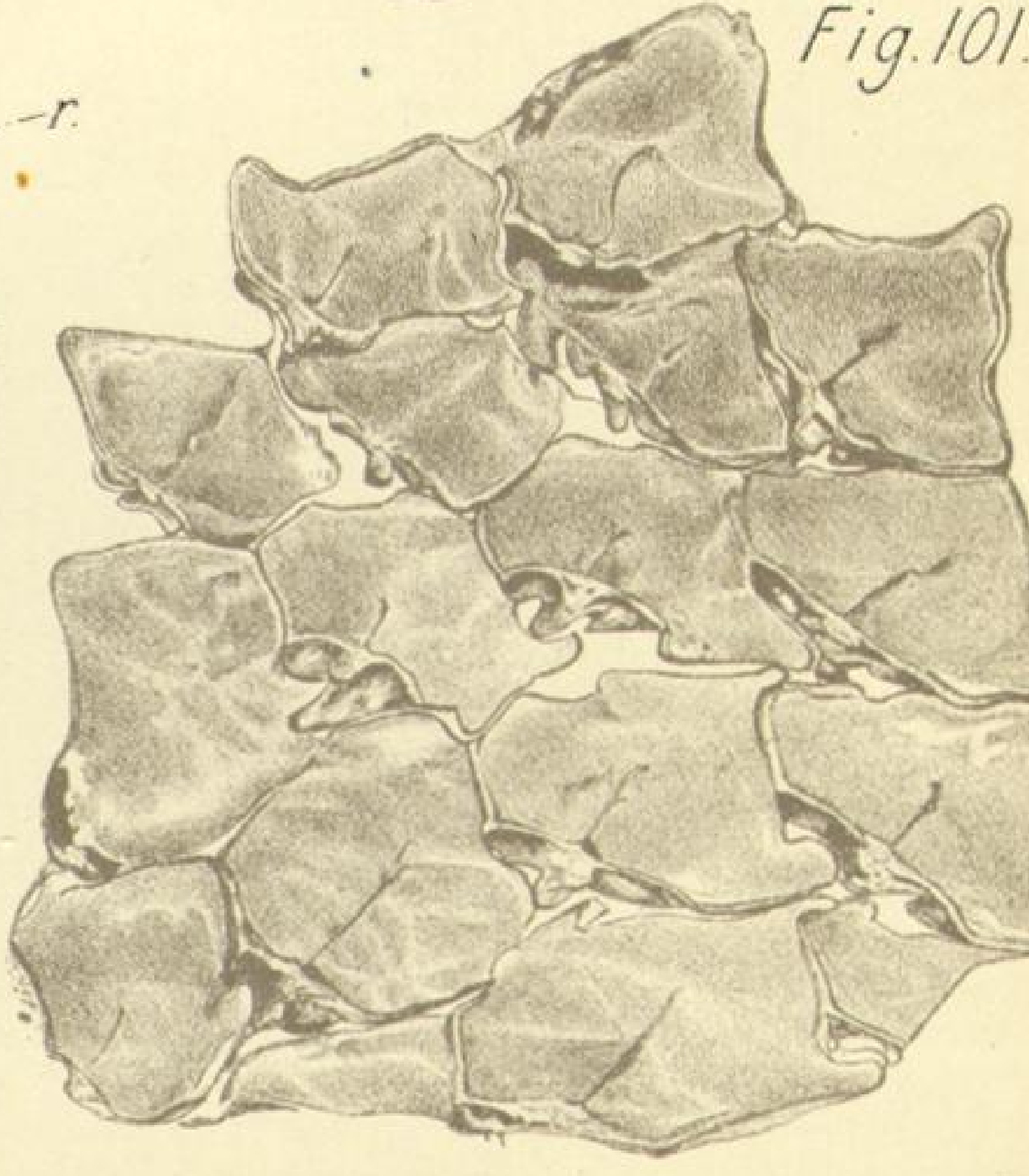
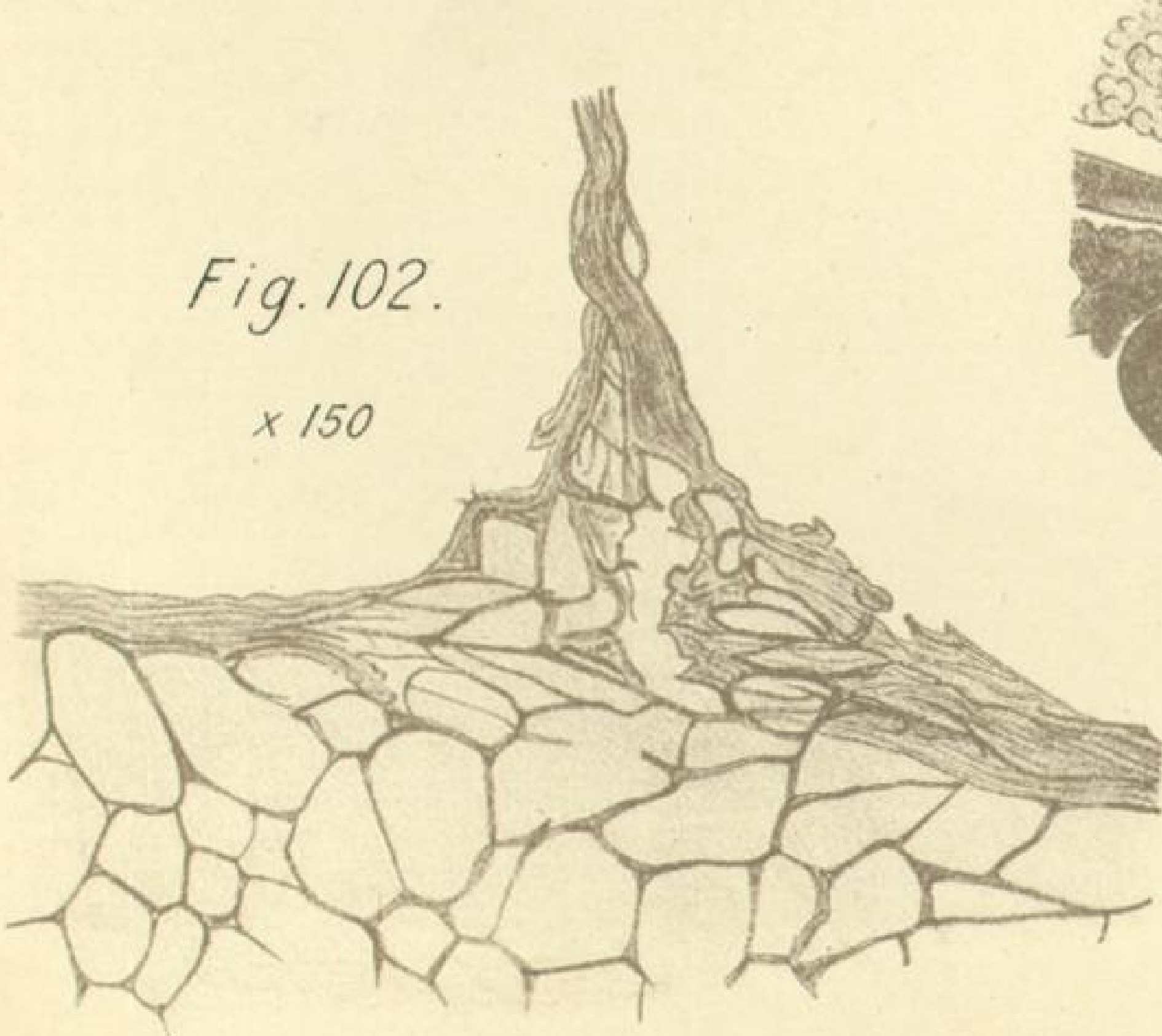


Fig. 102.



Figs 93-100. LEPIDODENDRON BROWNII. SCHPR.
Figs 101-102. LEPIDODENDRON SP. HOUGH HILL.
Fig. 103. LEPIDODENDRON BROWNII.

PLATE 48.

Lepidostrobus Brownii, Schpr.

Fig. 93. Wall of sporangium from a tangential section of the cone (No. 7 in the Museum series of tangential sections): it shows the outer sclerotic series of cells (*scl.*), with several layers of thin-walled cells within. (× 150.)

Fig. 94. From a photograph of part of a transverse section of the cone, showing three sporangia, with the upward projecting sub-archesporial pad as a median ridge (*r.*). (× 4½.)

Fig. 95. From a photograph of a tangential section of the cone.

Fig. 96. Drawing of a sporangium in tangential section of the cone with its sporophyll (*sp.*), slightly diagrammatic. *r.* = sub-archesporial ridge; *v.b.* = vascular bundle; *p* = processes rising from the ridge. (× 8.)

Fig. 97. Part of a radial section of the cone showing a small part of the base of the sporangium; *r.r.* = the sub-archesporial ridge, together with the processes (*p.p.*) which rise from it. (× 40.)

Fig. 98. The ridge (*r.*) as seen in tangential section of the cone (compare figs. 95, 96), showing on a larger scale the processes (*p.*) which project far upwards into the mass of spores. (× 40.)

Fig. 99. A sporangium from the apex of the cone, cut tangentially (compare fig. 95). The sporangium was not fully matured, and showed very large processes (*p*) springing from the sub-archesporial ridge, and continuous upwards towards the upper wall of the sporangium. (× 40.)

Fig. 100. Another such, with its sporophyll. (× 40.) Figs. 99 and 100 are taken from slide No. 9 of the tangential series in the British Museum.

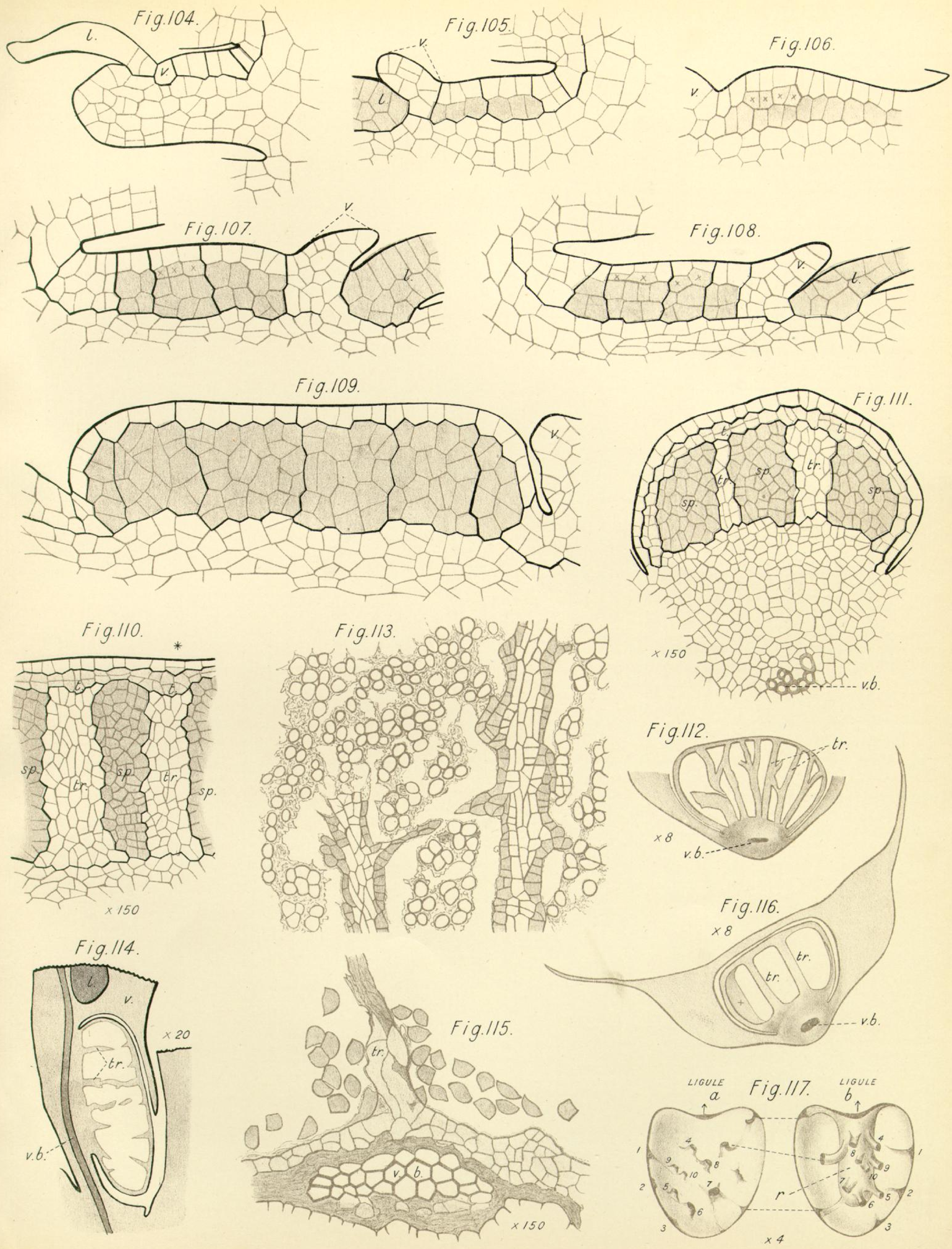
Lepidostrobus, sp., Hough Hill.

Fig. 101. From a photograph of a *Lepidostrobus* from Hough Hill, supplied by Mr. Lomax, and cut tangentially. The sporophylls and sporangia are easily seen, while each sporangium shows a dark process rising from the slightly convex sub-archesporial pad, and extending far upwards into the sporogenous mass. (× 4½.)

Fig. 102. The base of one of these processes seen under a higher power, and showing the cellular structure of the lower part, though this structure is lost upwards. (× 150.)

Lepidodendron Brownii, Schpr.

Fig. 103. Similar section from Schimper's smaller cone, in the British Museum, showing ridge (*r.*) and processes (*p.p.*) (× 20.)



Figs 104 - 117. ISOETES LACUSTRIS. L.

PLATE 49.

Isoetes lacustris, L.

L. = ligule; *v.* = velum; *t.* = tapetum; *tr.* = trabeculæ; *sp.* = sporogenous tissue; *v.b.* = vascular bundle.

Fig. 104. Part of radial section of a plant which has traversed a young leaf in median longitudinal section, the upper (adaxial) surface bears a rather regular layer of cells, as yet not divided periclinally; these are the parent cells of the sporangium. (× 300.)

Fig. 105. These cells are represented in an older state, having divided by both periclinal and anticlinal walls; the inner archesporial cells are shaded. (× 300.)

Fig. 106. A similar section, showing addition of cells (×) resulting from repeated periclinal division of superficial cells to the archesporium. (× 300.)

Figs. 107, 108. Older sporangia with archesporium shaded. (×) = cells believed to have been added by subsequent periclinal division of superficial cells. (× 300.)

Fig. 109. A much older sporangium, already developing as a microsporangium, in similar section, showing the sporogenous tissue as a connected and undifferentiated band. (× 300.)

Fig. 110. Part of an older microsporangium, in similar section, showing the potential archesporium differentiated into trabeculæ (*tr.*) and sporogenous masses (*sp.*), while the tapetum is also clearly defined: at (*) is an extra periclinal division in the wall. (× 150.)

Fig. 111. Transverse section of a sporophyll and microsporangium; *v.b.* = vascular bundle of sporophyll. Compare tangential sections of sporangia of *Lycopodium* (figs. 33, 43, 64, 65). (× 150.)

Fig. 112. A microsporangium drawn under low power to show the irregularity of the trabeculæ. (× 8.)

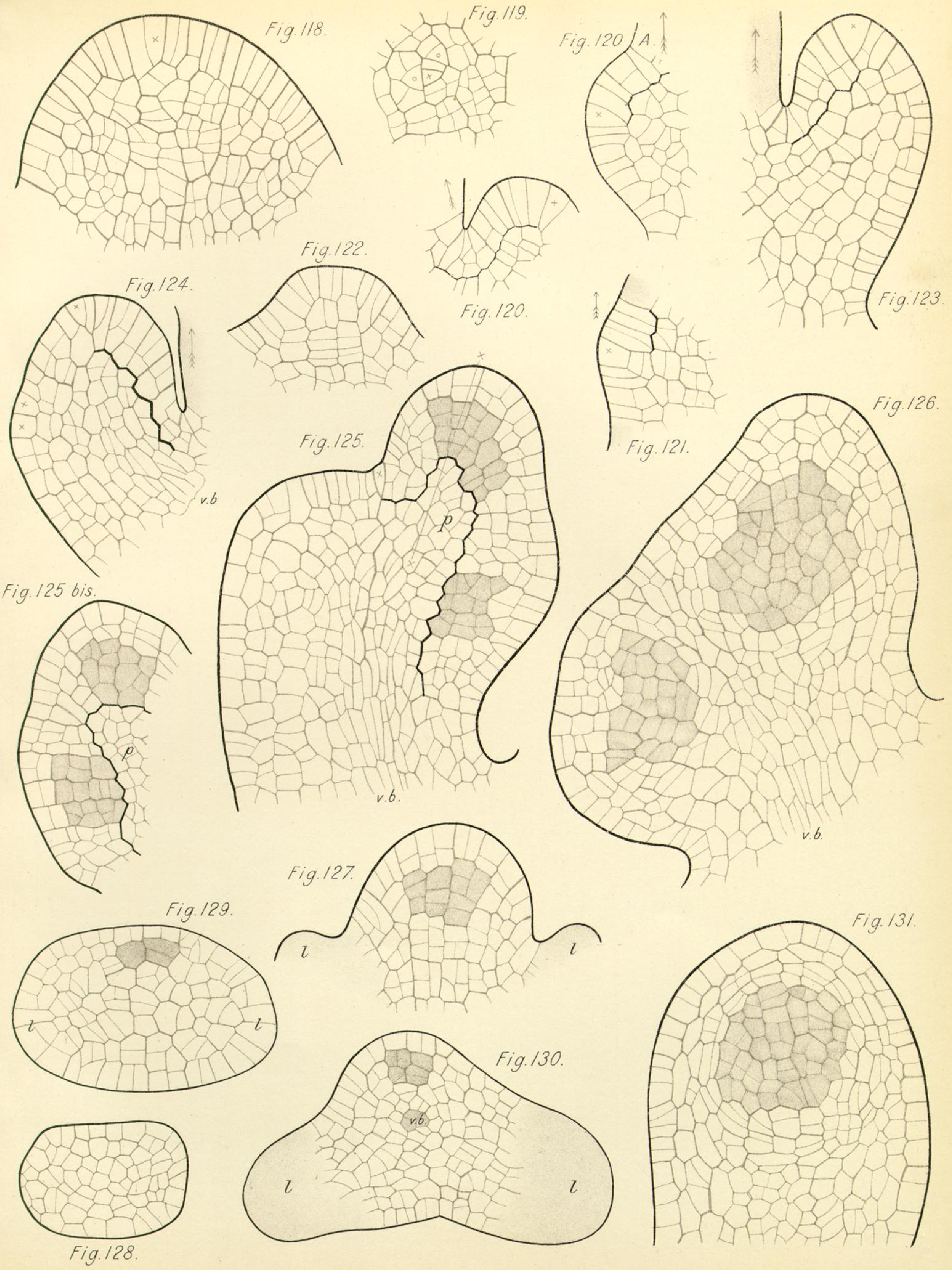
Fig. 113. Shows the structure of the trabeculæ, as well as their irregularity; the superficial layer has developed as a tapetum, which is shaded. (× 150.)

Fig. 114. A microsporangium in longitudinal section. (× 20.)

Fig. 115. The base of one of the trabeculæ of an almost mature microsporangium, still showing cell-structure in its lower part, but disorganized above. (× 150.) Compare fig. 102 of *Lepidostrobus*.

Fig. 116. Transverse section of a sporophyll with a megasporangium, from which the spores have been removed; the trabeculæ are apparently regular.

Fig. 117, *a* and *b*. A megasporangium which has been so cut as to remove the upper wall (*a*), from which the trabeculæ project into the cavity of the sporangium; (*b*) is the remainder of the sporangium, *r.* = the ridge, or sub-archesporial pad, which is to be compared with the similar part in *Lepidostrobus* (fig. 94, *r.*); it is from this ridge that the irregularly disposed trabeculæ arise. (× 4.)



Figs 118 – 131. TMESIPTERIS TANNENSIS BERNH.

PLATE 50.

Tmesipteris tannensis, Bernh.

Fig. 118. Median longitudinal section of the apex of a strongly growing stem, showing an initial cell (x), but a rather irregular disposition of the segments. (× 150.)

Fig. 119. Apical meristem of the axis of *Tmesipteris* as seen from above: (x) = initial cell, (o) = secondary initials. (× 150.)

Figs. 120 (A and B), 121. Young leaves, in radial section of a bud, showing the way in which they originate on the axis. (× 150.)

Fig. 122. A young leaf as seen in transverse section of the axis. (× 150.)

Fig. 123. A more advanced leaf, probably vegetative; at all events it shows as yet no clear indication of bearing a synangium. (× 150.)

Fig. 124. A very young synangium arising on the adaxial surface of a leaf which is closely similar to fig. 123. In this figure, as also in figs. 120–123, the basal line is more heavily marked. Compare the later figures also. (× 150.)

Fig. 125. Sporophyll bearing a much older synangium; the apical cell (x) may still be seen; the basal line is darkly marked as before, and the sporogenous masses are shaded. (× 150.)

Fig. 125, *bis*. Another specimen of the same, showing very regular disposition of the tissues. (× 150.)

Fig. 126. An older synangium in radial section. (× 150.)

Fig. 127. A vertical section along a line x, x, as shown in fig. 125; l, l are the leaf-lobes. (× 150.)

Figs. 128–130. Transverse sections of sporophylls of successive ages, so cut as to traverse the lower sporangium. l, l = leaf-lobes in fig. 130. (× 150.)

Fig. 131. Transverse section of an older sporangium. (× 150.)

Fig. 132.

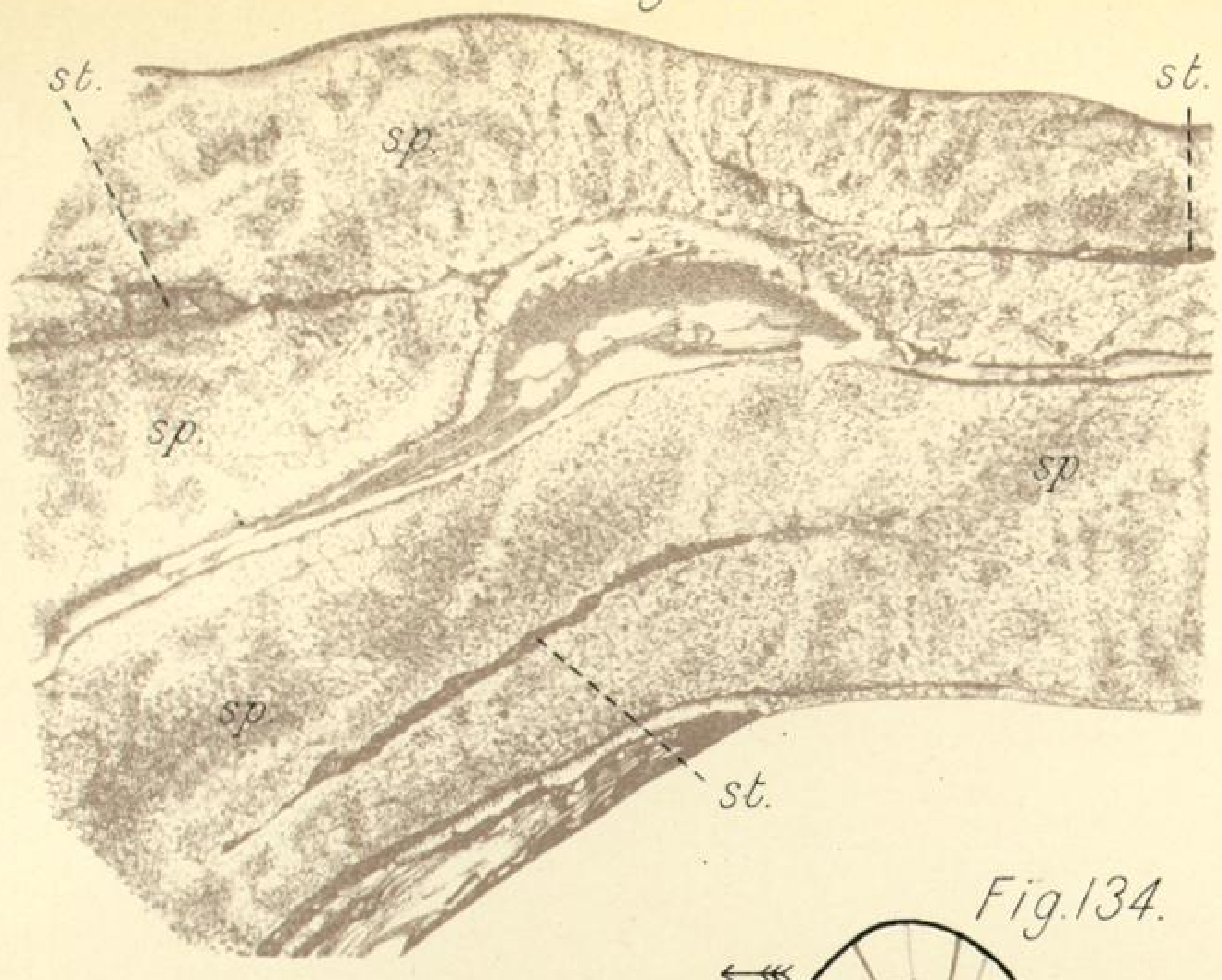


Fig. 131. bis.

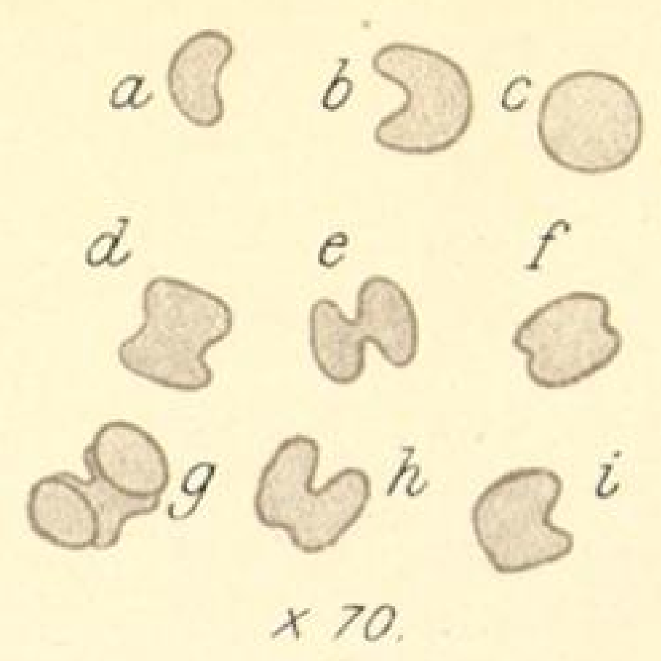


Fig. 133.

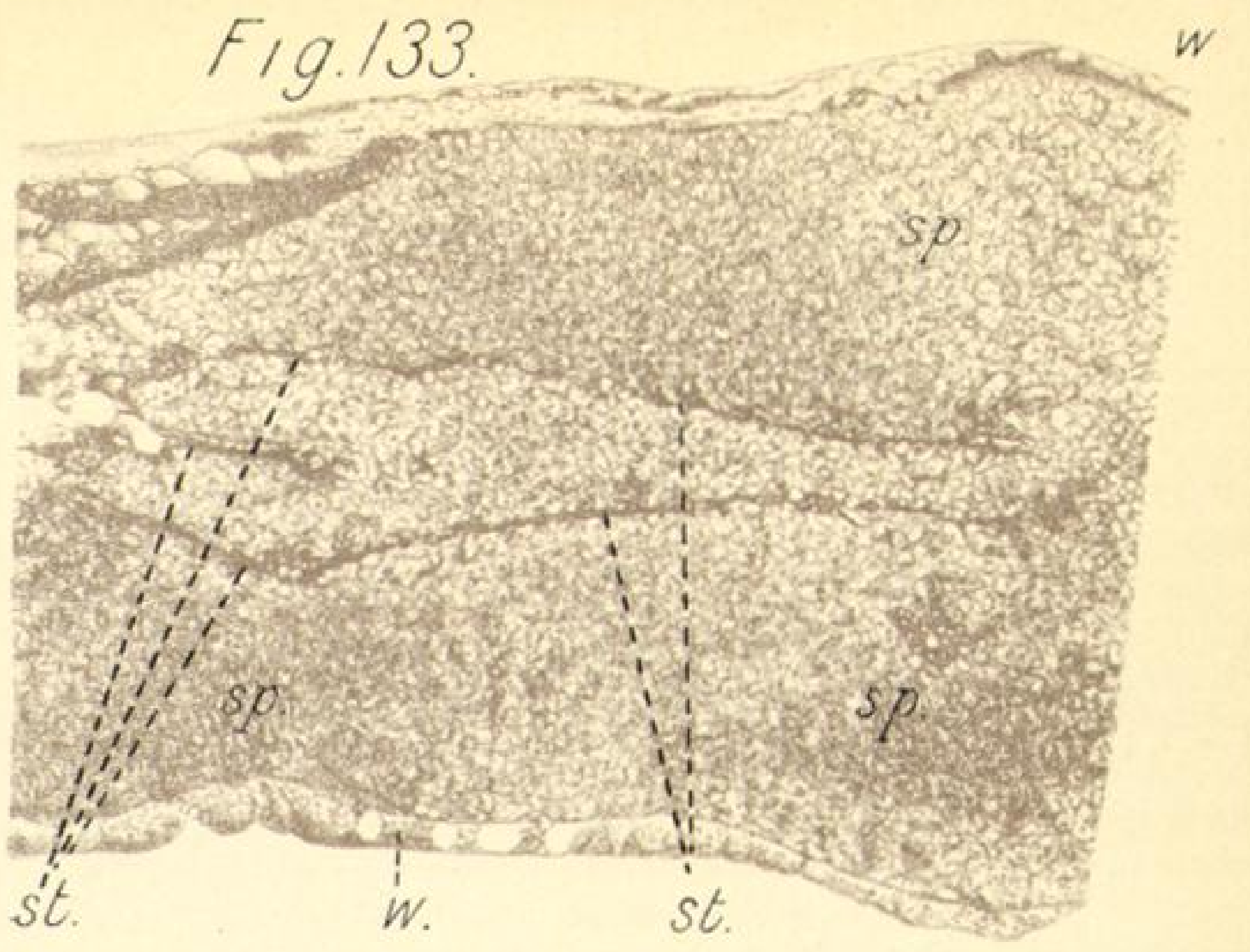


Fig. 135.

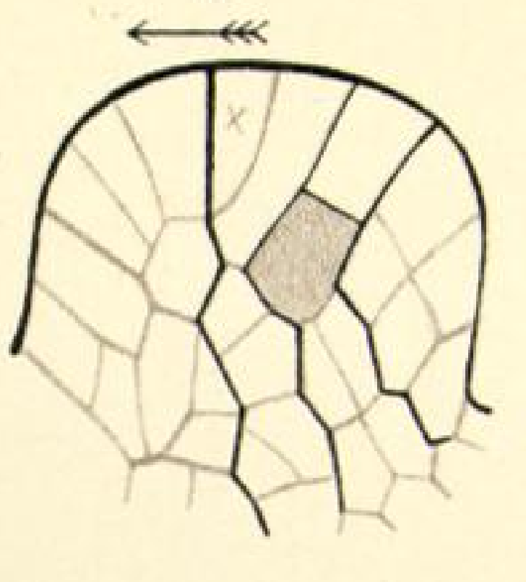


Fig. 134.

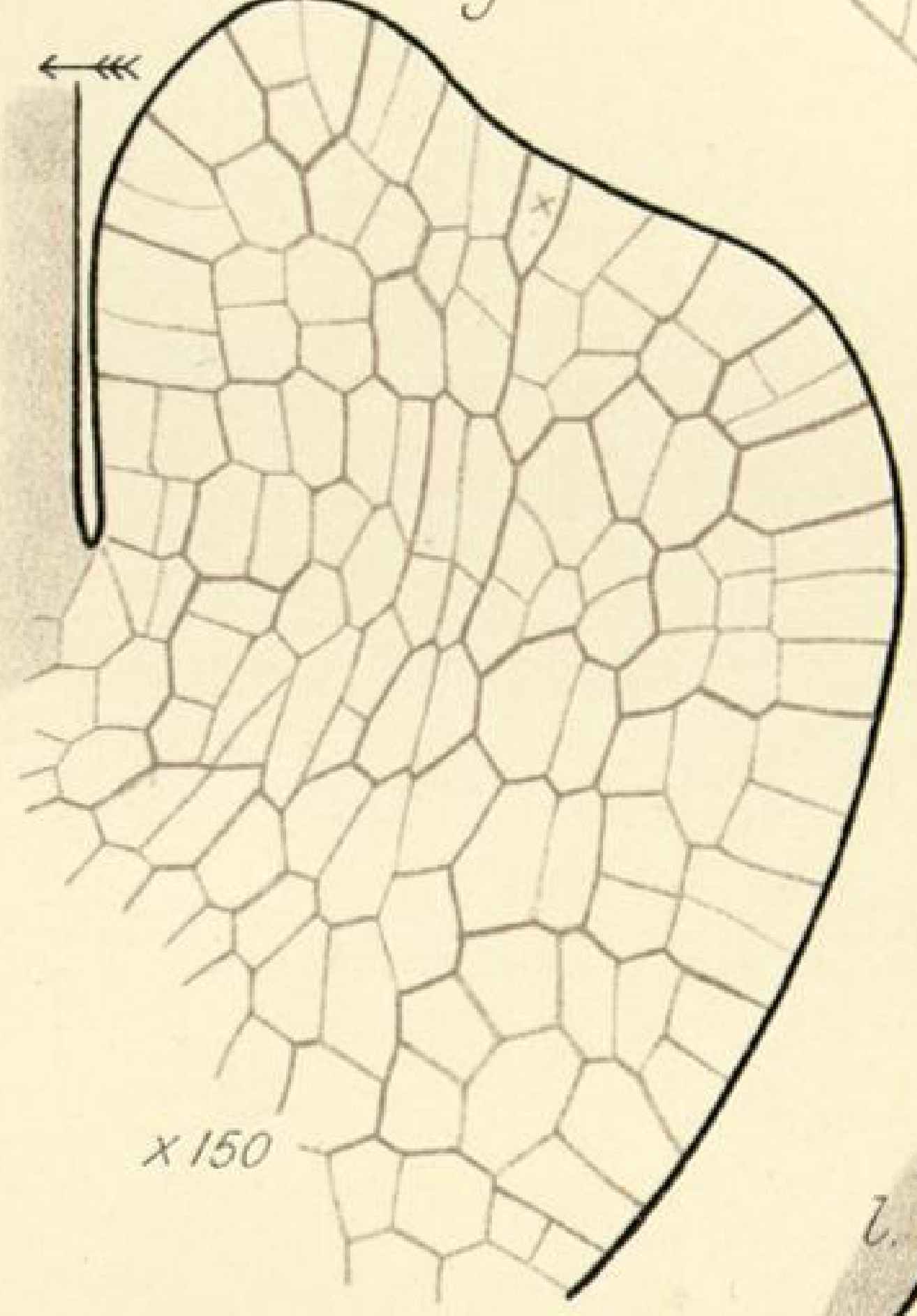


Fig. 136.

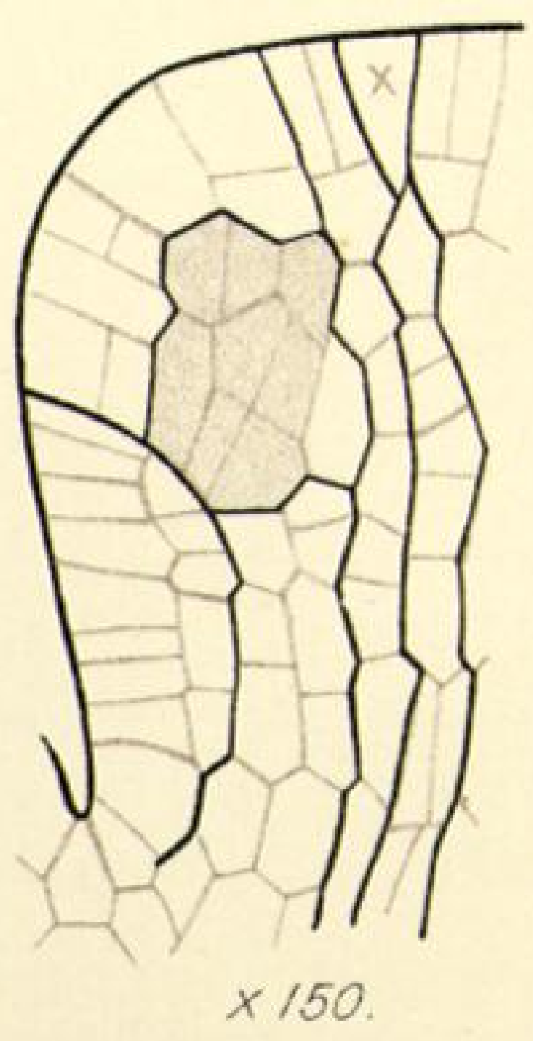


Fig. 137.

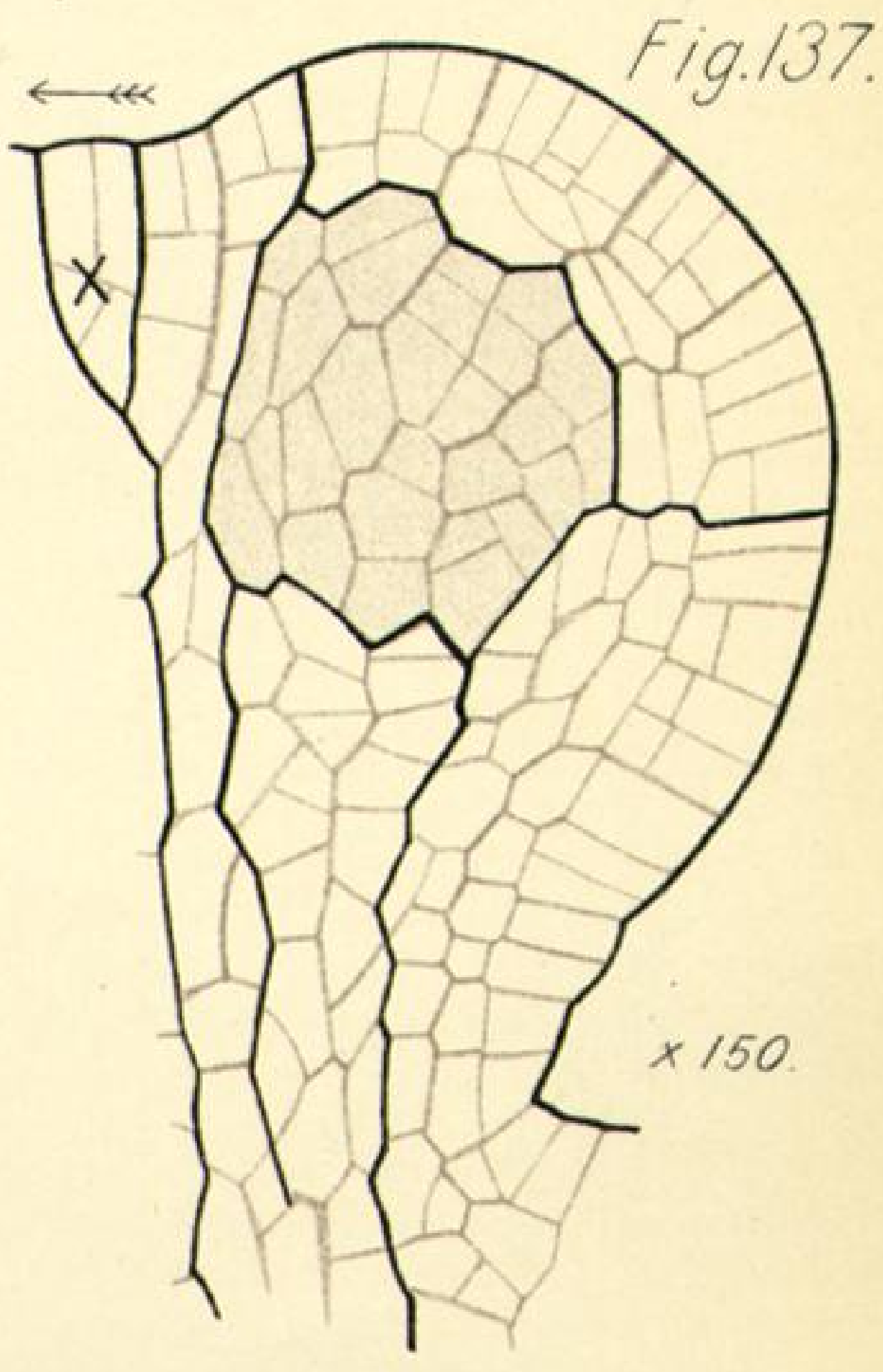


Fig. 138.

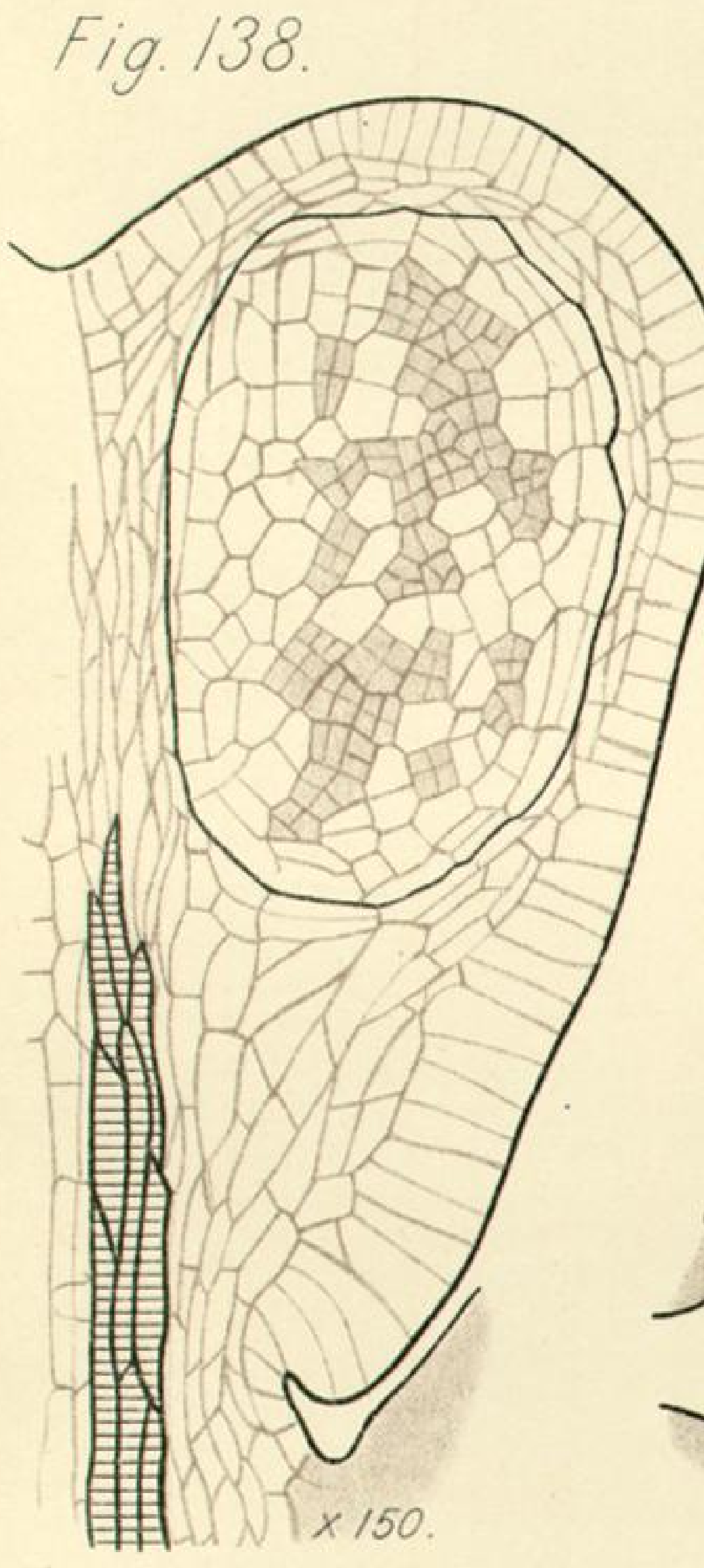


Fig. 140.

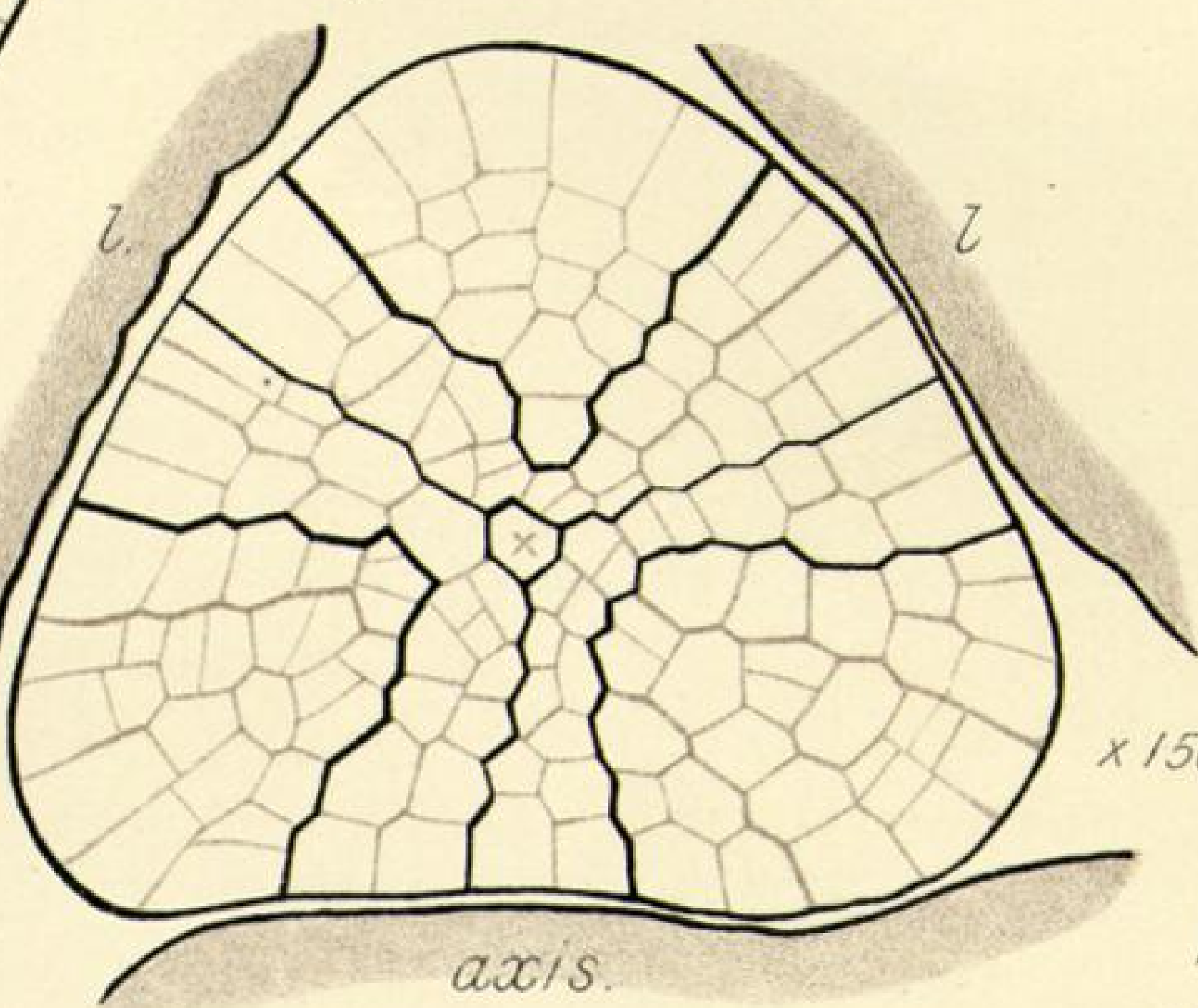


Fig. 139.

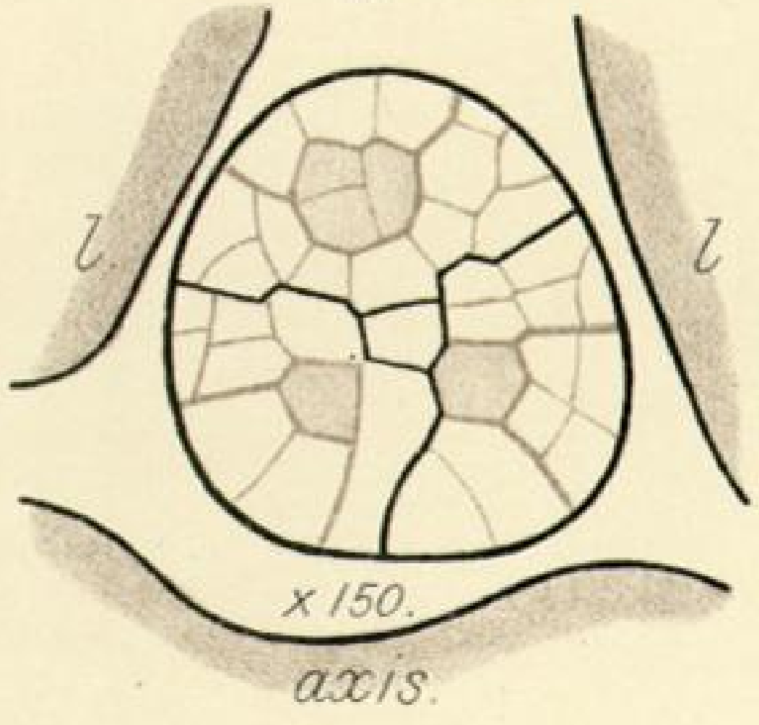


Fig. 141.

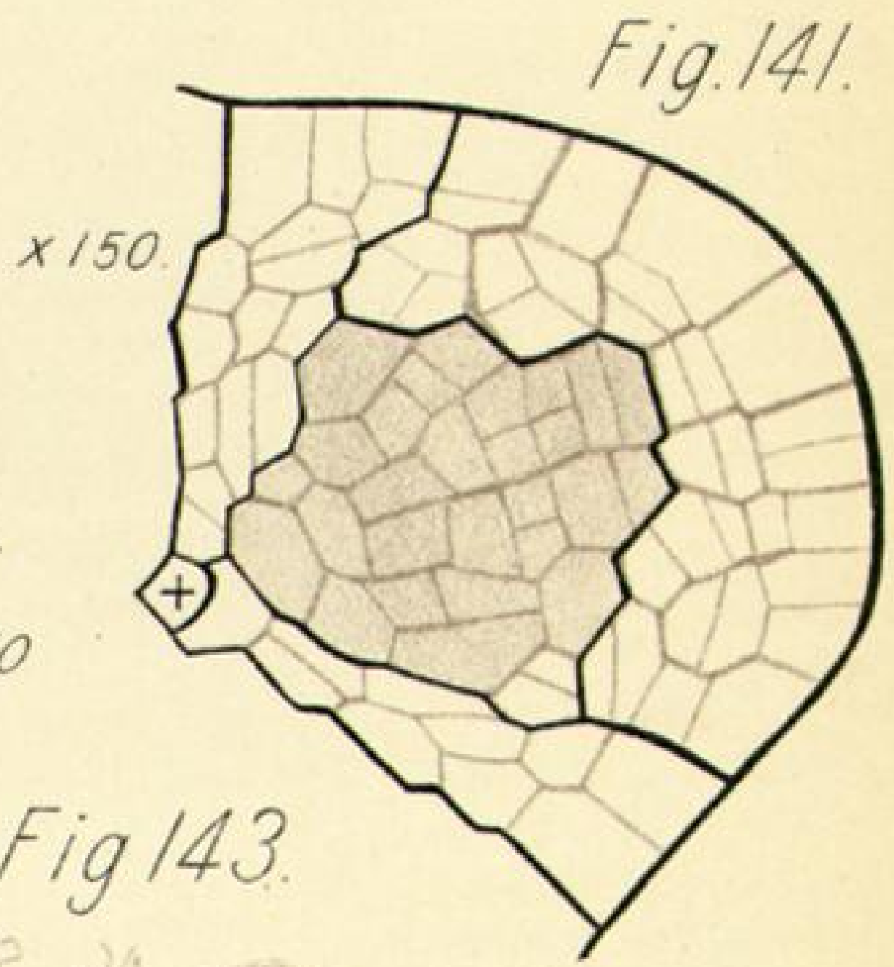


Fig. 143.

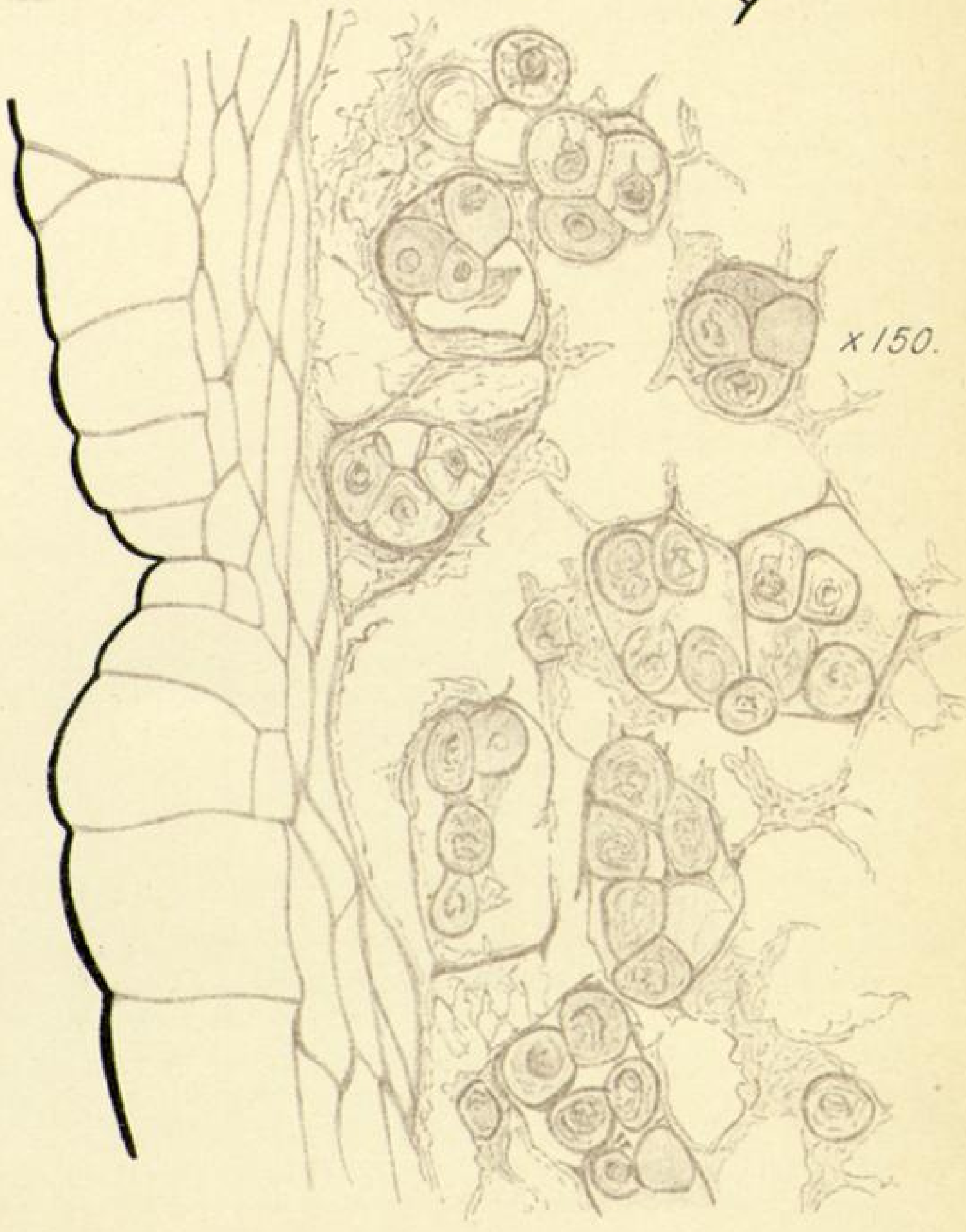


Fig. 144.

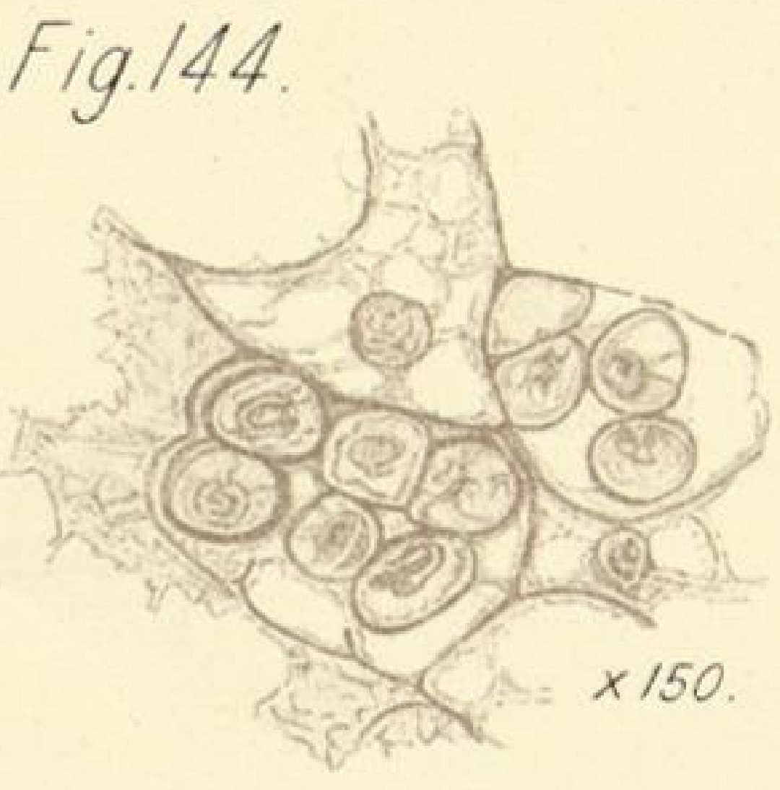


Fig. 142.

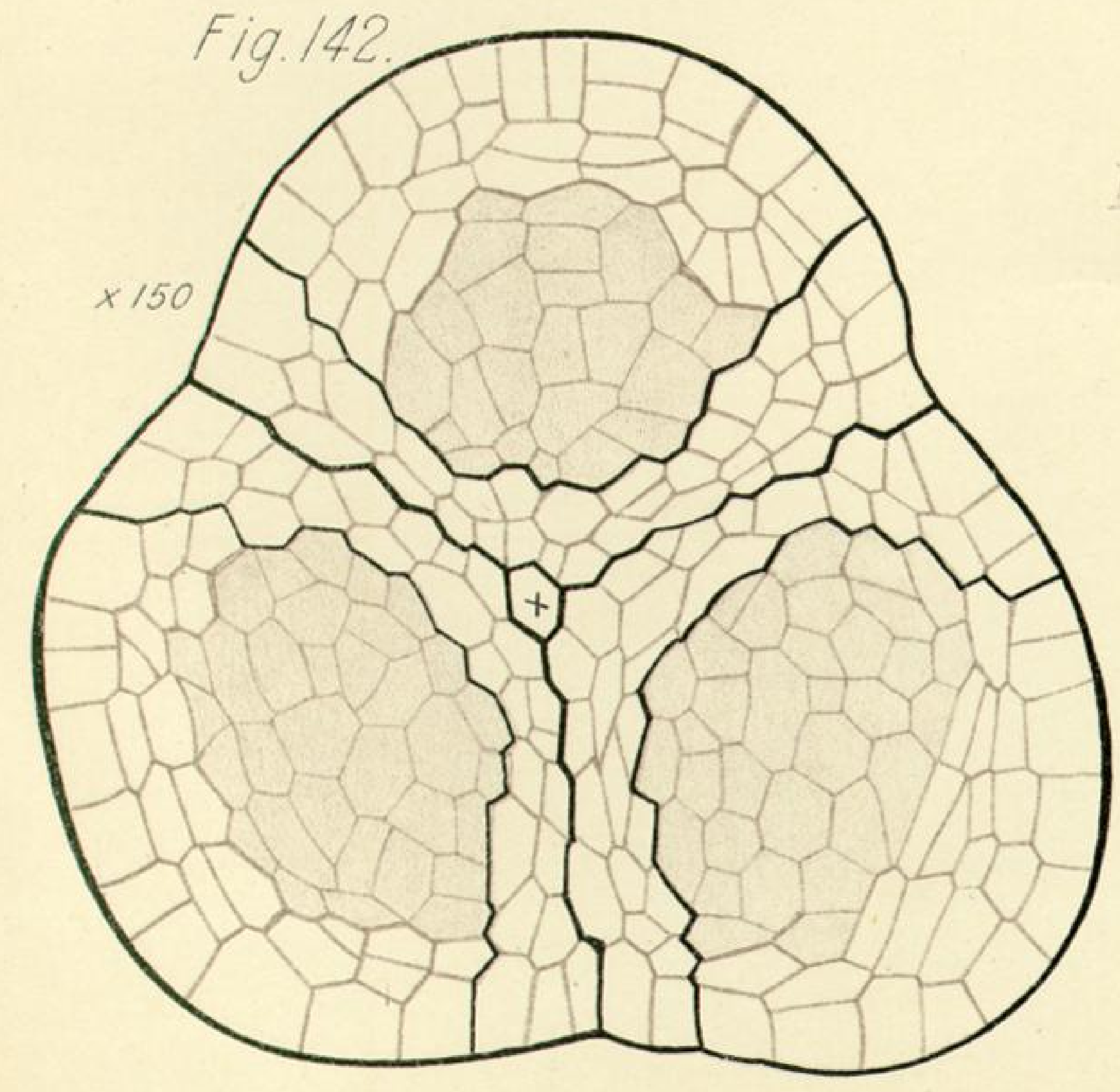
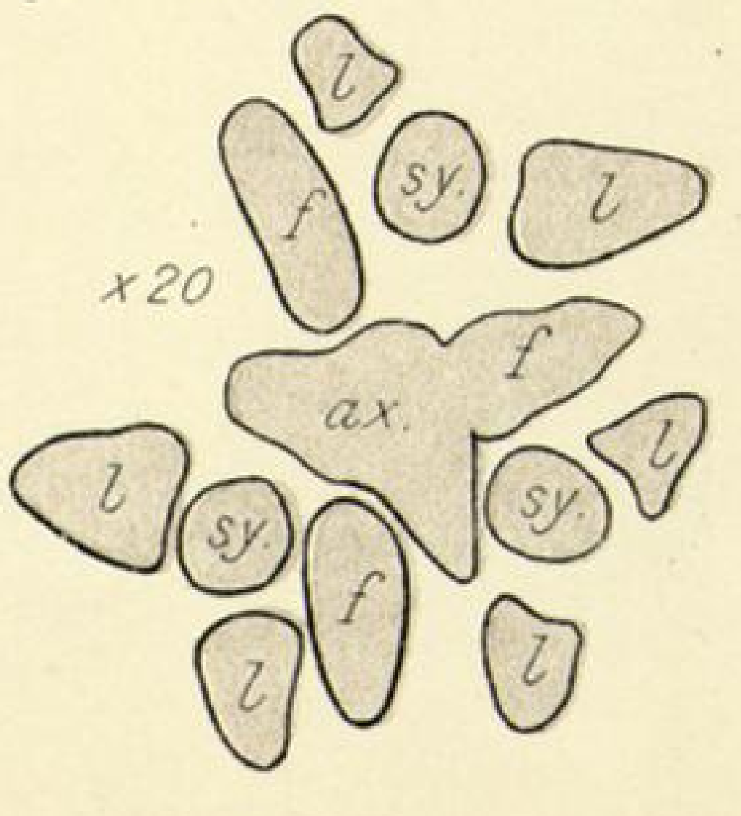


Fig. 145.



Figs 132. 133. LEPIDODENDRON.
Figs 135-144. PSILOTUM TRIQUETRUM. SW.
Fig. 145. TMESIPTERIS TANNENSIS. BERNH.

PLATE 51.

Fig. 131, *bis.*, *a–i*, spores from one normal synangium of *Tmesipteris*; *a* is the usual type; *b–i* show various abnormal forms, which appear to result from incomplete division of the tetrads.

Lepidostrobus, sp.

Fig. 132. From a photograph of a transverse section of a strobilus, showing part of two sporangia, which have been traversed in a plane above the sub-archesporial pad, but so as to cut through the sterile projections. These take the form of plates, which appear as dark streaks (*st.*), continuous for a considerable distance in a radial direction through the sporangium. There may be one such streak or plate of sterile tissue, as in the lower sporangium of fig. 132, or two less regular ones, as in the upper sporangium. The section shown in this figure has been slightly oblique: *sp.* = spores almost mature.

Fig. 133. A similar section showing three sterile plates (*st.*), which projected upwards into the mass of spores (*sp.*).

Psilotum triquetrum, Sw.

Fig. 134. Median longitudinal section of a sporophyll. (× 150.) Compare figs. 124 and 125 of *Tmesipteris*.

Fig. 135. Vertical section of a very young synangium, so as to traverse one of the three loculi. (× 150.)

Fig. 136. Ditto, older. (× 150.)

Fig. 137. Ditto, older. (× 150.)

Fig. 138. Ditto, older, on a lower scale. (× 100.) The cells shaded are the actual sporogenous cells.

Fig. 139. Transverse section of a synangium, rather older than that in fig. 135. (× 150.) *l*, *l* = leaf-lobes.

Fig. 140. Ditto, older. (× 150.)

Fig. 141. Ditto, one sporangium. (× 150.)

Fig. 142. Ditto, older. (× 150.)

Figs. 143, 144 illustrate the disorganization of certain cells of the sporogenous tissue, without forming spores. (× 150.)

Fig. 145. Transverse section through a sporangiferous bud of *Tmesipteris*. *ax.* = axis, *f.* = foliage leaves, *l.* = lateral lobes, *sy.* = synangia. (× 20.)

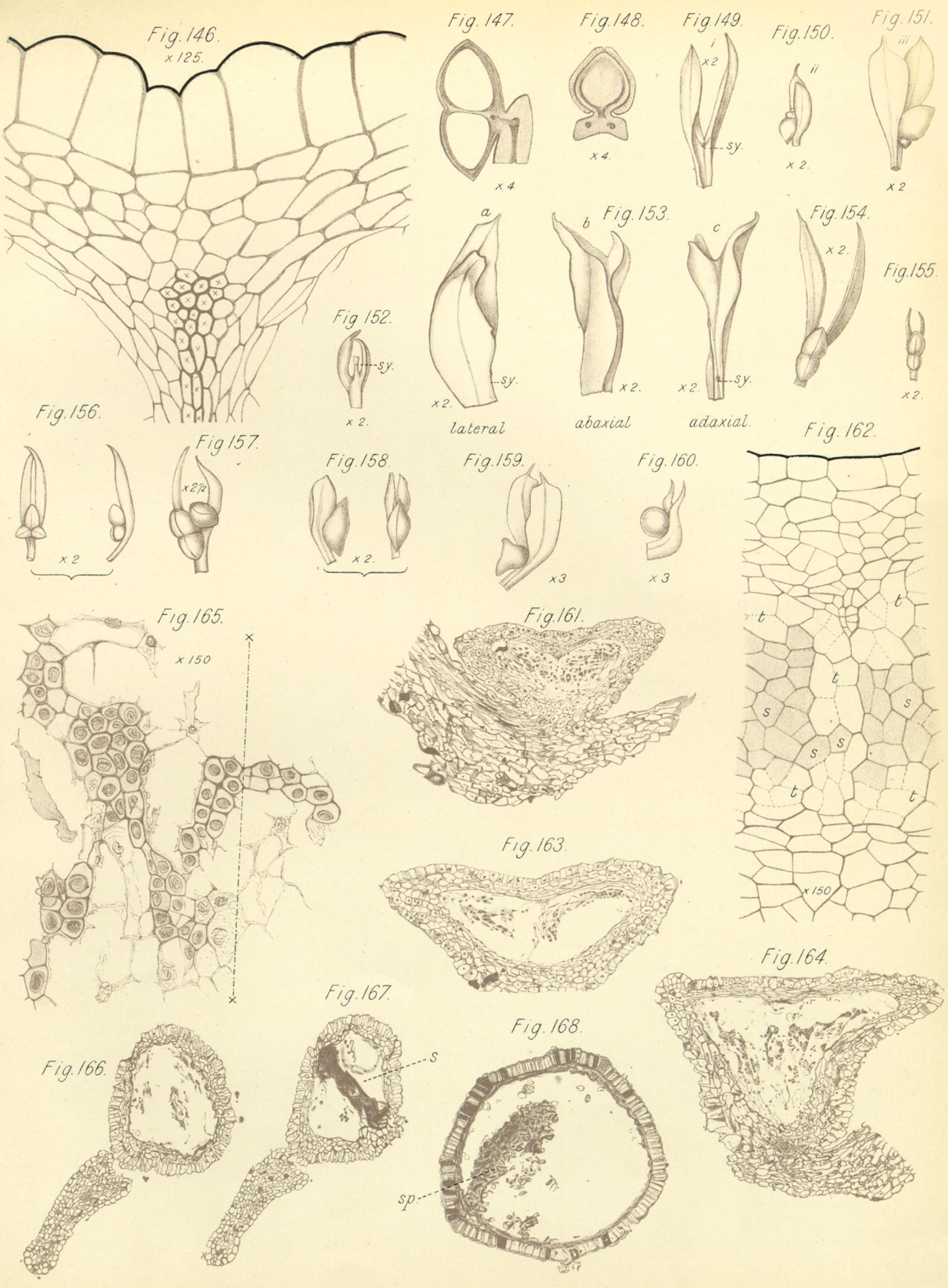


Fig. 146.
x 125.
Fig. 147.
x 4
Fig. 148.
x 4.
Fig. 149.
i
x 2
sy.
Fig. 150.
ii
x 2.
Fig. 151.
iii
x 2
Fig. 152.
sy.
x 2.
a
b
c
Fig. 153.
sy.
x 2.
x 2.
x 2.
sy.
lateral
abaxial
adaxial
Fig. 154.
x 2.
Fig. 155.
x 2.
Fig. 156.
x 2
Fig. 157.
x 2½
Fig. 158.
x 2.
Fig. 159.
x 3
Fig. 160.
x 3
Fig. 162.
t
t
t
s
s
s
s
s
t
t
x 150
Fig. 165.
x 150
x
x
Fig. 161.
Fig. 163.
Fig. 164.
Fig. 166.
Fig. 167.
s
Fig. 168.
sp

Figs. 146–168. TMESIPTERIS TANNENSIS. BERNH.

PLATE 52.

Tmesipteris tannensis, BERNH.

Fig. 146. Part of a radial section through a mature synangium, showing the groove between the sporangia, and the insertion of the septum. (× 150.)

Fig. 147. Radial section through a mature synangium, showing the vascular bundles. (× 4.)

Fig. 148. Section in the plane of the septum, showing the course of the vascular branches up the margin of the septum. (× 4.)

Fig. 149. A "double leaf," with abortive synangium (*sy.*). (× 2.)

Fig. 150. A synangium with the upper loculus abortive. (× 2.)

Fig. 151. Ditto, with lower loculus abortive. (× 2.)

Fig. 152. Ditto, with correlative growth, in place of the abortive synangium, inserted on adaxial face. (× 2.)

Fig. 153. Abnormal sporangiophore (*a*) in lateral, (*b*) in abaxial, (*c*) in adaxial view; *sy.* probably represents the abortive synangium. (× 2.)

Fig. 154. A normal sporangiophore from the middle of a fertile zone. (× 2.)

Fig. 155. A sporangiophore from the limit of a fertile zone, with very small leaf lobes. (× 2.)

Fig. 156. A sporangiophore with trilocular synangium. (× 2.)

Fig. 157. Ditto, but less regular. (× 2½.)

Fig. 158. Ditto, with synangium showing no transverse groove. (× 2.)

Fig. 159. Ditto, of type shown in section in fig. 164. (× 3.)

Fig. 160. Ditto, synangium of spherical form, shown in section in fig. 168. (× 3.)

Fig. 161. Median section through a synangium of type shown in fig. 158, with continuous sporogenous mass.

Fig. 162. Detailed drawing from a similar section, showing the tissue, where the septum should normally be present, developing as sporogenous cells (*s.*) and tapetum (*t.*). (× 150.)

Fig. 163. Synangium similar to fig. 161, rather more advanced.

Fig. 164. Synangium similar to that of fig. 159 in radial section, showing no septum; the cavity is filled with sporogenous and tapetal cells.

Fig. 165. Part of these contents drawn in detail from another section of the same series; the line *x*, *x*, shows where the septum would normally be, while a chain of sporogenous cells stretches continuously across it. (× 150.)

Figs. 166, 167. Two transverse sections, the one (fig. 167) higher up, the other (fig. 166) lower down in the same synangium. Fig. 166 shows no septum. Fig. 167 shows a septum cut through, which, therefore, only extended part way downwards into the cavity, from the upper wall of the synangium.

Fig. 168. Transverse section through the spherical synangium shown in fig. 160. No septum is present.

The figs. 132, 133, 161, 163, 164, 166–168 are from photographs kindly prepared for me by Mr. J. REID.